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Separation of the Species of Arborvitae Leaf Miners in New Brunswick (Lepidoptera: Yponomeutidae and Gelechiidae)¹

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Introduction

In 1950 work was started in New Brunswick to obtain information on the biology, control, and damage caused by the arborvitae leaf miners. At that time all damage was attributed to the arborvitae leaf miner, *Argyresthia thuiella* (Pack.). After the first season's work four species were recognized. Adults submitted to the Systematic Unit, Entomology Division, Ottawa, were identified as *Argyresthia thuiella* (Pack.), *A. freyella* Wlshm., *Recurvaria thujaella* Kft., and a new species of *Argyresthia* later described by Brower (1) as *aureoargentella*. With the exception of *A. thuiella*, insufficient material was available for complete morphological studies, so work was based on finding suitable characters to separate the species in the late larval, pupal, and adult stages.

This is the first of two papers on the arborvitae leaf miners. The second deals with the biology and control.

Description of Stages

Practically all the material for study was obtained by individual vial rearings. The vial best adapted for this work was a 6 x 1 inch with a solid bottom and with a solid cork, a fine mesh screen, or cotton top.

Infested foliage was collected in the field as required. The leaf scales were teased off the mine exposing the larva, which was described, and the head capsule measured. The scales were then folded back and the foliage containing the mine placed in a vial. The mines were re-opened periodically for re-examination. Mortality was exceedingly high, sometimes reaching 90 per cent, so that relatively few larvae completed their development.

The pupae were easily separated and efforts were made to rear pure stock which would have greatly facilitated work. Identified pupae and adults were placed in cages but all attempts failed to produce sufficient progeny for the work required.

Argyresthia thuiella (Pack.)

Larva

Head capsule widths were measured and plotted to determine the number of instars. Six peaks were apparent but there was no distinct grouping of the instars. However, measurements taken on individual larvae for two or more successive stadia indicated the six instars as shown in Table 1.

Sixth Instar.—The head capsule, cervical shield, and anal plate are black to brown. The body colour varies from green to brown with the following colour variations: light green, later changing to dark green, green with reddish-brown tinges along the posterior edge of each body segment, brown mottled with green or reddish flashes, and occasionally solid brown. Regardless of the colour combination the cervical shield is very prominent and solid (Fig. 1). The setal pattern is shown in Fig. 5. The mandibles have five teeth, sometimes only four clearly defined.

¹Contribution No. 317, Forest Biology Division, Science Service, Department of Agriculture, Ottawa, Canada; based on a thesis presented to the Faculty of the Graduate School at the State University of New York, College of Forestry, in partial fulfilment of the requirements for the degree of Doctor of Philosophy, June, 1956.

TABLE 1
Mean Width and Range of Head-Capsule Measurements of *A. thuiella* by Instars

Instar	Number	Mean width in mm.	Range in mm.
1	98	0.104	0.088-0.110
2	108	0.145	0.132-0.165
3	103	0.183	0.165-0.209
4	39	0.227	0.209-0.253
5	146	0.304	0.275-0.330
6	77	0.380	0.330-0.396

The labrum has a shallow notch with seta M_1 on the same level or slightly higher than M_2 .

The male gonads are clearly visible through the dorsum of the fifth abdominal segments of the late instar larvae and this is a reliable sex character (Figs. 8 and 9).

Pupa

Average length 3.5 mm., width 0.73 mm. The initial colour is green, changing to brown. An important distinguishing character is the posterior tip which is curved with a definite cremaster bearing ten curved hooks (Fig. 13). The pupa is always found in the mine.

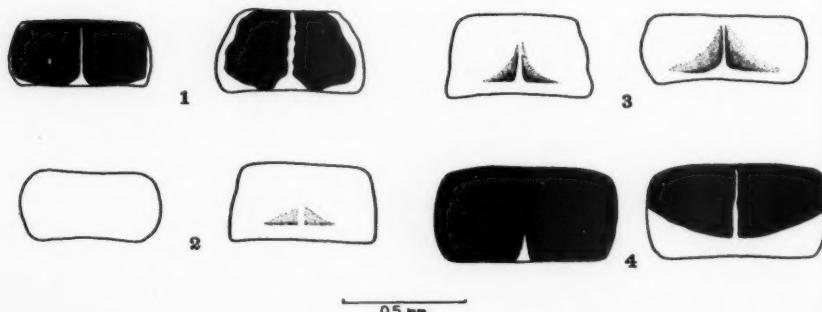
Adult

The original description is given by Packard (5) so note is made only of essential features. The moth is small with an average wingspread of about 8 mm. The body and forewings are white with brown markings. On the distal end of the wing in the middle edge is a conspicuous black spot. The wing venation is shown in Fig. 16. The female has a stout abdomen, rounded at the end. The male abdomen is more slender and pointed.

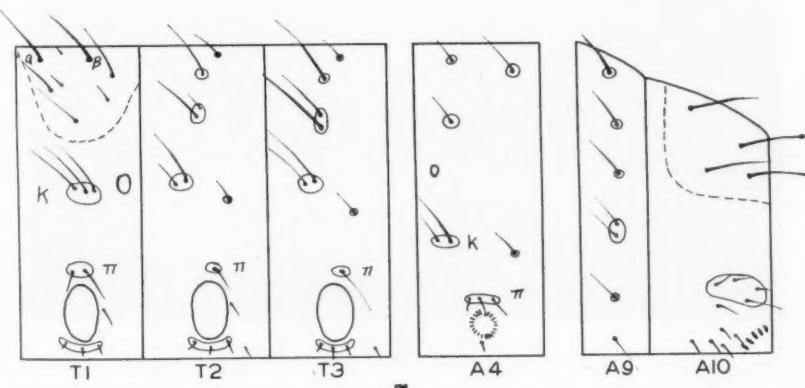
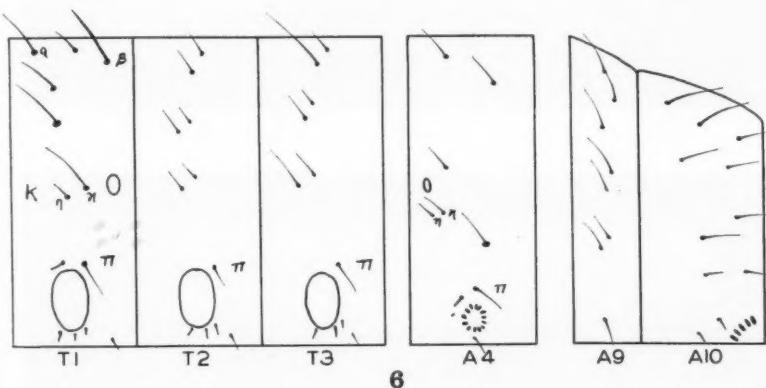
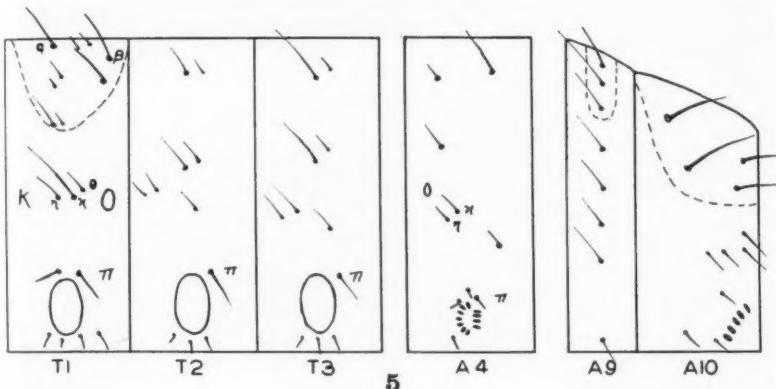
Argyresthia aureoargentella Brower

Larva

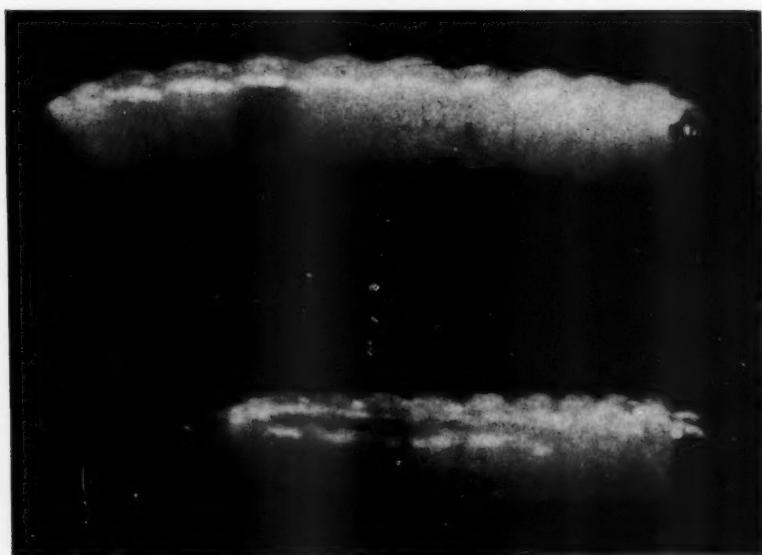
Insufficient material was available to determine the head widths of each instar, but observations and a limited number of measurements indicated six instars.



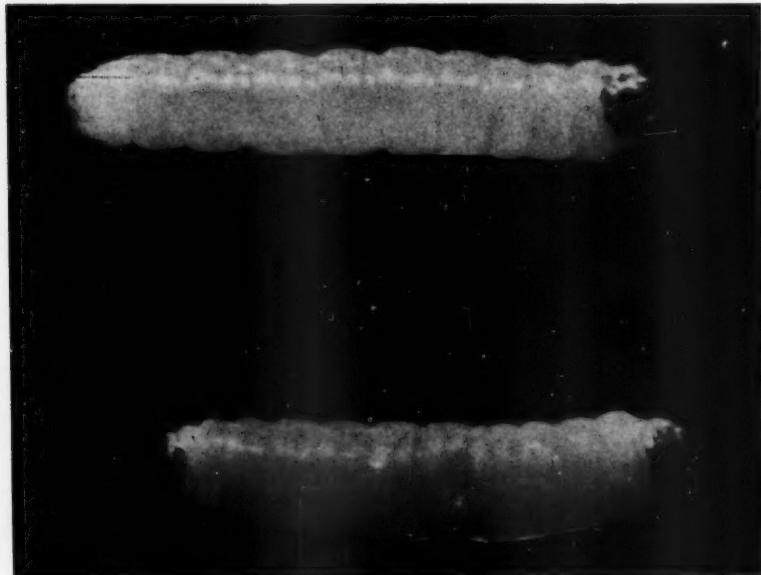
Figs. 1-4. Cervical shields of last instar arborvitae leaf miner larvae; 1, *A. thuiella*; 2, *A. aureoargentella*; 3, *A. freyella*; 4, *R. thujuella*.



Figs. 5-7. Setal patterns of last instar arborvitae leaf miner larvae; 5, *A. thuiella*; 6, *A. aureoargentella*; 7, *R. thujaeella*.

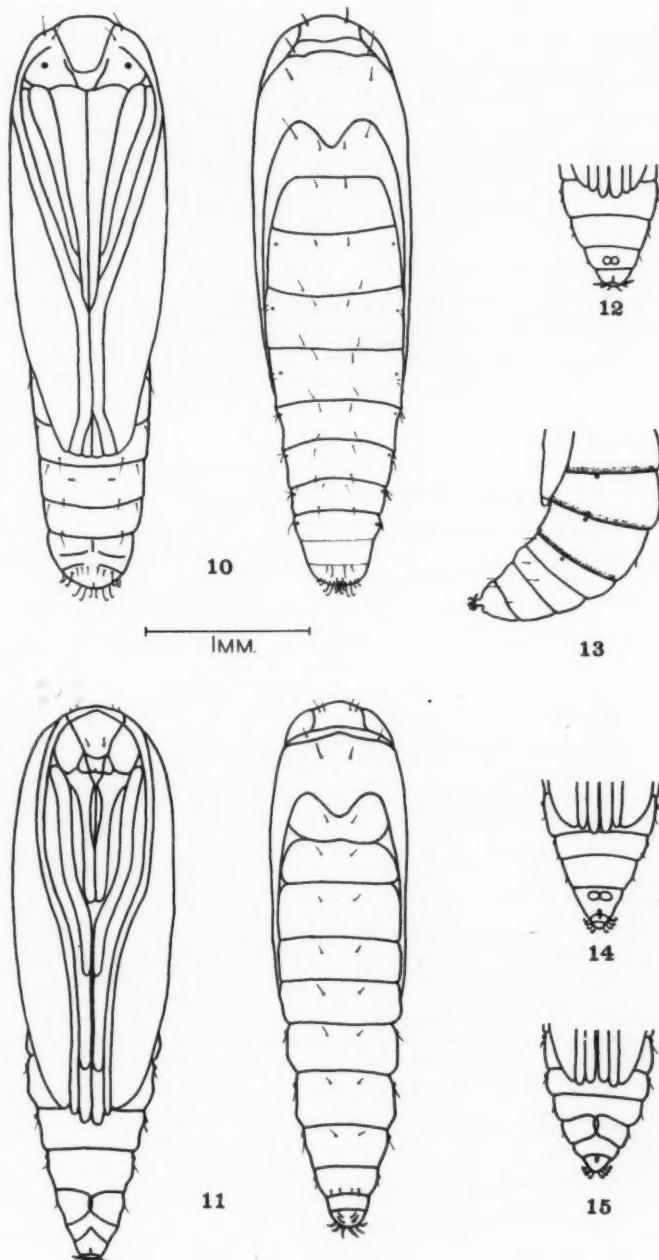


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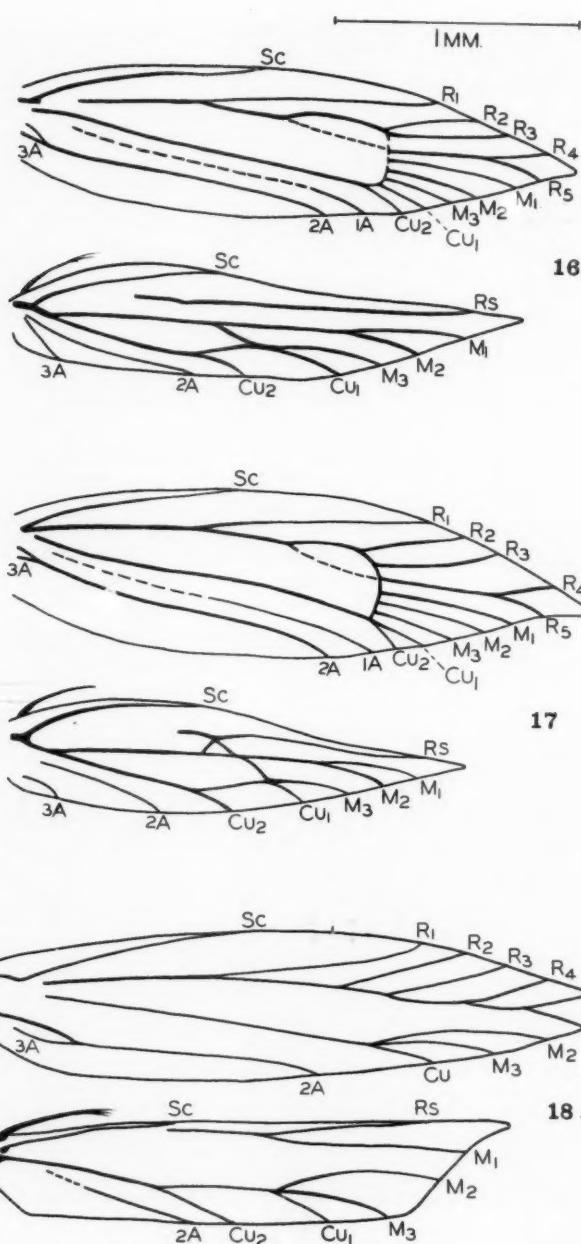


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Figs. 8-9. Sex characteristics of *A. thuiella* larvae: 8, male larvae showing dark dorsal spot on fifth abdominal segment; 9, female larvae.



Figs. 10-15. Arborvitae leaf miner pupae: 10, *R. tbuella*; 11, 12, *A. aureoargentella*; 13, *A. tbuella*; 14, 15, *A. freyella*.



Figs. 16-18. Wing venation of arborvitae leaf miners: 16, *A. thuiella*; 17, *A. aureoargentea*; 18, *R. thujaella*.

Ultimate Instar.—The head is green to brown in colour, width about 0.40 mm. The cervical shield is the same colour as the body or granular, not solid as in *A. thuiella* (Fig. 2). The body is light to dark green, sometimes yellowish-green, the anal plate is the same colour as the body, or light brown. The setal pattern (Fig. 6) is similar to *A. thuiella* with one exception; Kappa group on the prothorax is bisetose. Fracker (3) states that in this family Kappa is always trisetose on the thoracic segments, but theta was not observed on any of the three larvae observed. The mandibles have five teeth, not as clearly defined as in *A. thuiella*. The labrum has a fairly deep notch with seta M₁ on the same level or slightly lower than M₂.

Pupa

Length is about 3.1 mm., width about 0.9 mm. The general appearance is similar to *A. thuiella* but the tip of the pupa is not curved. The cremaster is rounded, not prominent, and bears ten straight hooks, six on the distal and two on each side. (Figs. 11 and 12).

Cocoon

The average length is 5.1 mm., and width 1.1 mm., and the length/width ratio 4.5. The cocoon is spindle shaped, white in colour, and is usually on the lower side of the branch surface (Fig. 19).

Adult

The small moth has a wing expanse of 7.5 to 9.0 mm. The thorax is white with golden shoulders. The forewing is golden with conspicuous silver bars and markings and a small dark apical spot. A full description is given by Brower (1). The wing venation is similar to *A. thuiella* with small variations (Fig. 17).

Argyresthia freyella Wlshm.

Larva

Observations and measurements on a limited amount of material indicated six larval instars.

Ultimate Instar.—The head capsule is green to brown with a head width of about 0.42 mm. The cervical shield is green with brown markings, and divided along the mid-dorsal line with the brown on either side fading into body colour (Fig. 3). The body is yellowish-green to green. The setal pattern is similar to *A. aureoargentella*. The mandibles have five teeth, the fifth almost obsolete in some specimens. The labrum has a pronounced notch, usually with more of an apex than the other species, and with seta M₁ usually lower than M₂.

Pupa

The average length is 3.1 mm., width about 0.9 mm. The initial colour is green, later changing to brown. The general appearance is similar to *A. aureoargentella* with one distinct difference. The cremaster is more projected and bears eight curved hooks, four on the distal and two on each side (Figs. 14 and 15).

Cocoon

The average length is 4.3 mm., width 1.5 mm., and the length/width ratio is 2.8. The cocoon is stout, spindle shaped, often irregularly oval, white in colour and speckled with brown (Fig. 20). The cocoons are usually on the underside of the foliage.

Adult

The small moth has a wingspread of 7 or 8 mm. The head and thorax are white. The forewings are golden with silver spots and bands. There is a distinct triangular black dot at the extreme apex. For full description see

Walsingham (6). The wing venation is similar to the other two species of *Argyresthia* with small inconsistent variations.

Recurvaria thujaella Kft.

Larva

Very few larvae were found in the field prior to 1953. In that year some material was available and the head widths of 81 larvae were measured. This small number was insufficient to define the number of instars or their range. A number of measurements on the same larvae for two or three instars provided measurements of the last three instars. Dyar's rule (2) was applied, using the last two instars as a basis. The calculated head widths did not coincide with the measurements available so the number of instars is not known, but there are at least five and possibly six.

Ultimate Instar.—The head width is about 0.50 mm. The head capsule is black, the cervical shield and anal plate brown. The body is reddish-brown to red. The setae rise from dark brown conspicuous verrucae. The anal comb is composed of a large pair of curved prongs with three smaller prongs on either side. The cervical shield is solid (Fig. 4). The setal pattern is shown in Fig. 7. The mandibles have five prominent teeth. The labrum has a shallow notch, and the sclerotized area extends above M_1 setae which are at a lower level than M_2 .

Pupa

The length is 3.8 to 4.5 mm., width 0.90 to 1.0 mm., and is brown in colour. The vertex of the head is rounded and smooth, tapering evenly to a broad, rounded anal end bearing more than ten slender curved hooks (Fig. 10). The pupa is always found in the mine.

Adult

The original description is given by Kearfott (4). The wingspan of about 10 mm. is greater than of the other three leaf miners. The head and thorax are creamy white. The forewings are creamy white with black patches and bands. The wing venation is shown in Fig. 18.

Feeding Patterns

Early in the study a difference was noted in the mining patterns. Although variations exist, general patterns have been established.

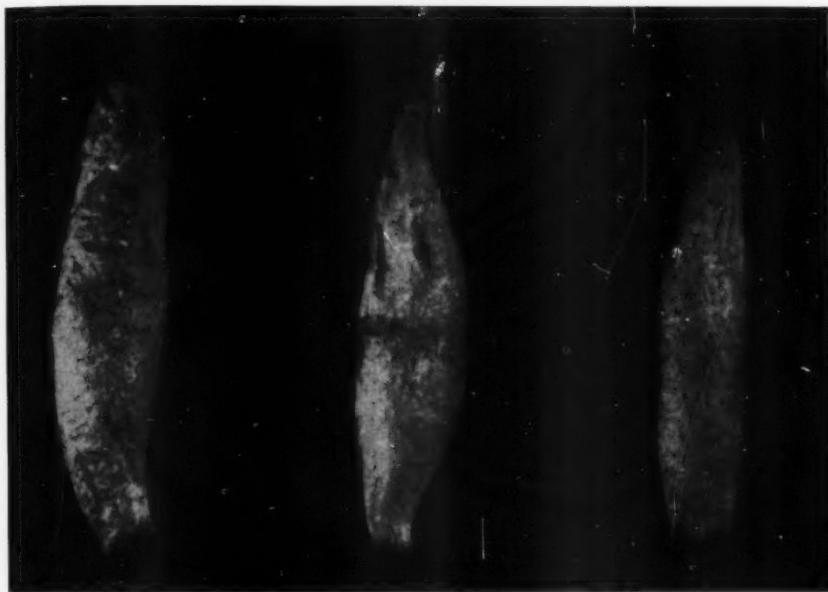
With few exceptions larvae of *A. thuiella* spend their entire life in one mine. All three leaf scales in a row are commonly mined (Figs. 21 and 22), but there are a few exceptions. The mines are kept relatively free of frass through frass ejection holes, which are covered with silk after use.

No difference was found between the mining patterns of *A. freyella* and *A. aureoargentella*. Mines usually extend down one side of the shoot, the outside and portions of the centre leaf scales being eaten (Figs. 23 and 24). Occasionally the pattern is similar to that of *A. thuiella*. Frass is usually left in the mines. There is an entrance and exit hole in each mine. The larvae occupy two or more mines during their development.

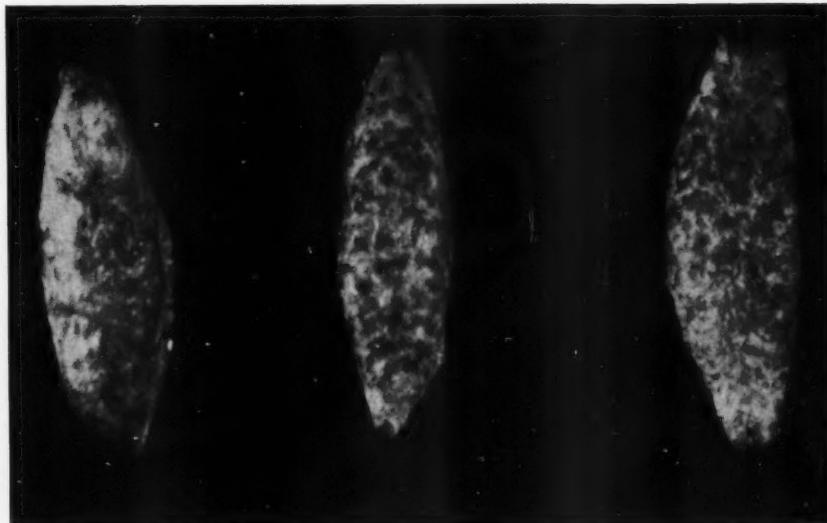
The *R. thuyaella* pattern is very similar to *A. thuiella* (Figs. 25 and 26). Most larvae spend their entire lives in one mine.

Discussion

The larvae of *R. thuyaella* are easily recognized by the red body, black head, anal comb, and the setae arising from verrucae. The three species of *Argyresthia* are not so easily separated. Setal patterns are of limited value, and there is too much variation and not enough clearly defined differences in the mandibles, labra, or the mining patterns to identify any species with certainty. The brown

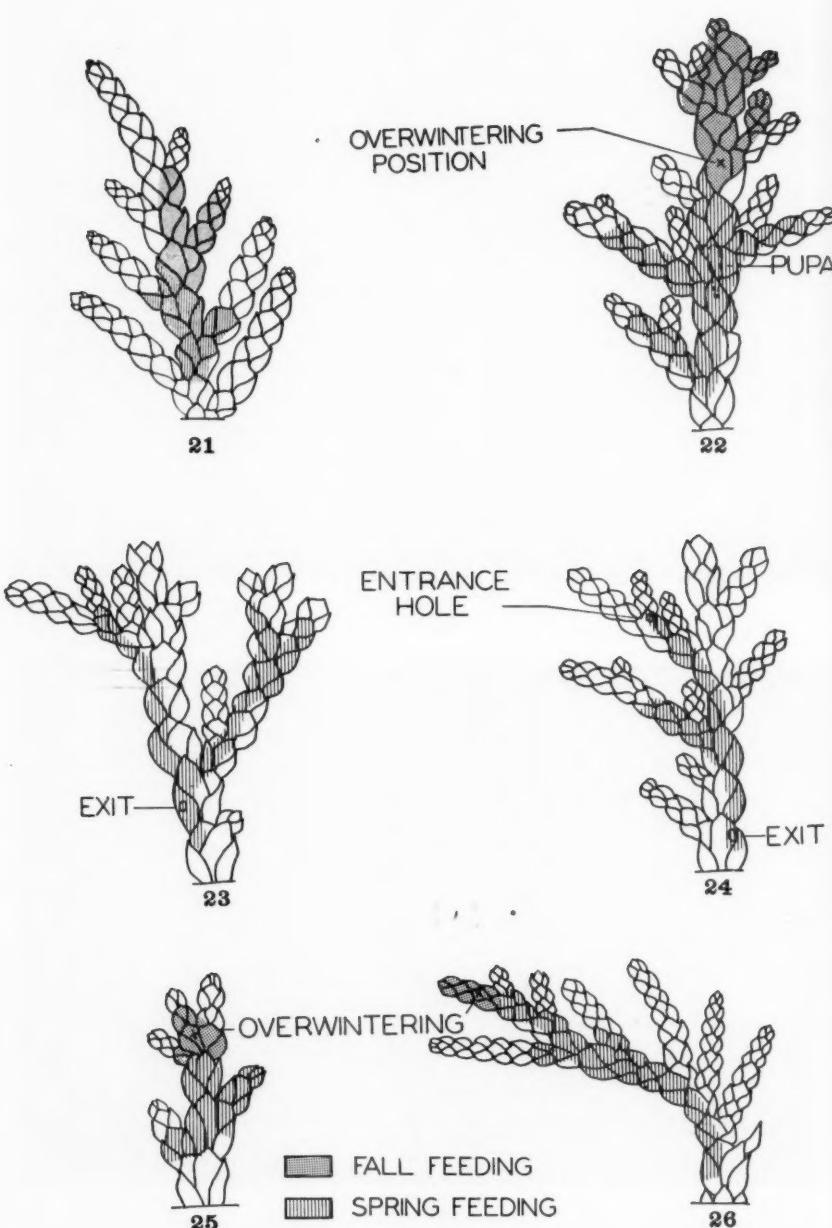


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Figs. 19-20. Arborvitae leaf miner cocoons showing differences in the shape and colour between the two cocoon spinning species: 19, *A. aureoargentella*; 20, *A. freyella*.



Figs. 21-26. Typical larval mining patterns of the arborvitae leaf miners: 21, 22, *A. thuiella*; 23, *A. freyella*; 24, *A. aureoargentella*; 25, 26, *R. thujaella*.

A. thuiella larvae can be easily identified, and those with the body colour other than brown can be distinguished by the brown to black head, dark anal plate, the brown transverse dorsal line on the 9th abdominal segment, and the solid brown to black cervical shield which is a consistent character.

The body colour of the two cocoon-spinning species is similar. Differences in the mandibles and labra vary too much for positive identification. The best character is the cervical shield which is always lacking or only granular in *A. aureoargentella*, whereas *A. freyella* has a partial shield divided along the mid-dorsal line.

The pupal stage can be more positively identified than any other. *A. thuiella* and *R. thuyaella* always pupate in the mine. The pupa of the former is smaller and the cremaster is prominent with ten curved hooks. *R. thuyaella* is larger, the end of the pupa is broad, rounded, and smooth with more than ten small slender curved hooks. The other two species spin cocoons on the surface of the foliage. The cocoon of *A. freyella* is shorter and wider, and is white speckled with brown spots. The cocoon of *A. aureoargentella* is cigar shaped and all white. In *A. freyella* the cremaster of the pupa has eight curved hooks compared with ten straight hooks for *A. aureoargentella*.

The golden wings with silver markings distinguish adults of the two cocoon spinning species from the other two. The silver markings of *A. freyella* are poorly developed, the bands sometimes broken, the markings duller, and the black apical spot prominent in contrast with the well defined bands and small apical spot of *A. aureoargentella*. These differences are best observed by comparing groups of adults. *R. thuyaella* adults are larger than those of *A. thuiella* and have oblique black bands in contrast with brown markings on *A. thuiella*. In cases of doubt the completely different wing venation gives unmistakable identification.

Summary

The larvae, pupae, and adults of *R. thuyaella* are easily distinguished from the other three species of leaf miners. All three stages of *A. thuiella* can be separated from *A. freyella* and *A. aureoargentella*. Separation of the latter two species is difficult in the larval stage, but they are easily identified either by the characteristically different cocoons or pupae. The moths of these two cocoon-spinning species are best separated by comparison.

Acknowledgments

I wish to thank R. E. Balch and W. A. Reeks, Fredericton, for their valuable guidance and assistance during the development of the study program. I wish to thank W. G. Wellington and R. R. Lejeune for their assistance in the preparation and criticism of this paper, and R. Banyard who did the original photographic work.

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Further Studies on the Mating Range of the Honey Bee, *Apis mellifera L.*

By D. F. PEER¹

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Abstract

Genetically-marked virgin queen honey bees were located at various distances up to 14.0 miles from an apiary stocked with genetically-marked drones in an area containing only these experimental bees.

Some matings occurred across distances up to 10.1 miles. With increasing distances from the drone source a decreasing percentage of queens mated successfully. Queens located at the drone source, 3.8 and 6.1 miles distant, began laying at approximately the same time. Those located 8.0 miles distant began laying later and those at 10.1 miles later still.

Introduction

The breeder's goal of releasing better strains of honey bees cannot be realized until he can control the drone population mating his queens. Under natural conditions this can be accomplished only through isolation. While the geneticists and foundation stock producers are able to select better strains, controlling matings by instrumental insemination, the majority of commercial stock breeders are unable to increase them because they cannot obtain pure matings naturally and instrumental insemination is too costly.

Several investigators (Sladen, 1920a, 1920b; Klatt, 1928, 1929, 1931, 1932; Roberts, 1944) have studied the problem of mating range. Peer and Farrar, 1956a, reviewed their work and further demonstrated that queens and drones are able to mate when their colonies are separated by distances up to six miles. Although this was the maximum distance tested, they stated that probably queens and drones are able to mate when separated by greater distances.

The experiments reported herein were conducted in an area containing only experimental bees to determine the maximum distance that queen colonies can be separated from drone colonies and still obtain matings. Conversely, these experiments would indicate the minimum distance required to isolate a mating apiary from other drone sources.

Methods

An experimental apiary was established near Whitney, Ontario, because the provincial colony registration records indicated that there were no bees located within 35 miles. The rolling terrain of the area is covered primarily with bush.

Genetically-marked stock was used to check the honey bee isolation of the area and also to determine whether the experimental queens mated with the experimental drones. The simple recessive mutation, cordovan (Mackensen, 1951), which produces brown or cordovan body pigment in place of black, was utilized. This mutation is particularly suitable because it does not affect mating behaviour (Peer, 1956b), and cordovan bees are easily distinguished from others. The production of cordovan worker offspring by the cordovan queens would be proof that they had mated to cordovan drones and also that the area was isolated from other drones.

The experiment was conducted during August and early September, 1955. Favourable weather conditions for mating predominated throughout this period.

Twenty colonies headed by mutant queens which produced only mutant drones were moved to the site. Mutant virgin queens were mated from droneless

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nuclei located in the experimental drone apiary and at various distances to the east of it.

The hybrid cordovan virgin queens were reared using a double graft technique. They were unrelated to the drones in the experimental apiary, and therefore would be expected to carry different lethal alleles (Mackensen, 1951). High viability was expected and obtained from matings of these queens and drones.

The five-frame mating nuclei were made queenless and the drone brood and adults removed by the following method: Queen excluder was placed over the entrance of each nucleus. Every bee was brushed from the combs and nucleus box onto the grass in front of the stand. The worker bees were able to reenter the nuclei, while the drones were excluded. Drone comb was scraped to the foundation to make certain that all eggs and larvae were destroyed. Examination of the nuclei the following day revealed that they were droneless.

Each of the nuclei received a 10-day-old queen cell. When examined two days later they all contained virgin cordovan queens. On the fifth day after the cells were introduced the nuclei were moved to the Whitney area, and the queen excluder guards removed from the entrances. The numbers of nuclei in the various locations and the distance separating each location from the drone site are shown in Table 1.

The nuclei were inspected for laying queens 15, 23 and 31 days after the virgins emerged. Queens not laying by the 31-day examination were considered to be unmated. The offspring were examined to determine with what type or types of drones each queen had mated.

Results

Table 1 presents a summary of the numbers of queens that mated at each of the seven locations. With increasing distance from the drone source a decreasing percentage of queens mated successfully. None of the queens at the 12.0 or 14.0 mile locations were able to find mates.

The successfully mated queens located at the drone source, 3.8 and 6.1 miles distant, began laying at approximately the same time. Those located at the 8.0 mile site began laying later and those at 10.1 miles later still.

All of the queens except one produced only cordovan offspring. This queen produced both cordovan and wild-type offspring in one of the nuclei located in the experimental drone apiary.

Discussion

The objective of this study was reached—that is, to determine the distance required to isolate a mating apiary from other drone sources.

It has been shown in the foregoing that some queens can mate with drones when their colonies are separated by 10.1 miles. Since none of the queens located 12.0 and 14.0 miles from the drones became mated, it may be concluded that few, if any, are able to mate across these distances. Furthermore, since the queens located at the 8.0 and 10.1 mile sites began laying later than those located at the drone source and the 3.8 and 6.1 mile sites, it is evident that the more distant queens were slower finding mates. Had there been a drone source in the vicinity of the distant nuclei, certainly the queens would have had no trouble finding mates. Likely, too, they would not have mated with any of the drones from the 20-colony cordovan apiary.

Unfortunately, this investigation gives no indication of the respective distances flown by drones or queens during mating.

The queen that produced both cordovan and wild-type worker offspring must have mated to at least one cordovan drone and at least one wild-type drone.

Probably the wild-type drone or drones came from one of the 20 cordovan drone colonies because previously they had been located in an apiary which also contained colonies with wild-type drones.

Commercial queen breeders, who wish to produce stock mated to known drone sources, should isolate their mating apiaries from other drone colonies by at least eight miles. In cases where such isolation cannot be obtained, all colonies within eight miles should be requeened with the same drone-producing stock used in the mating apiary. Obviously, too, the larger the drone population flying from the mating apiary the less the chance of mismatching.

Summary

Genetically-marked virgin queen honey bees, *Apis mellifera* L., were located at various distances up to 14.0 miles from an apiary stocked with genetically-marked drones. Some matings occurred across distances up to 10.1 miles.

TABLE 1
Mating range of the honey bee, Whitney, Ontario, 1955

Miles Separating Queens From Drones	Number of Queens	Number of Queens Laying			Per Cent of Queens Laying
		15th Day	23rd Day	31st Day	
0.0*	9	9	—	—	100
3.8	9	8	—	—	89
6.1	9	6	—	—	67
8.0	12	0	3	2	42
10.1	12	0	0	3	25
12.0	11	0	0	0	0
14.0	11	0	0	0	0

*Virgin queens located in drone apiary.

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The Bark Beetle Complex Associated with Lodgepole Pine Slash in Alberta

Part III—Notes on the Biologies of Several Predators with Special Reference to *Enoclerus sphegeus* Fab. (Coleoptera: Cleridae) and Two Species of Mites¹

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The most important predators found with broods of *Ips pini* (Say) and *Ips perroti* Sw. belong to the orders Coleoptera, Diptera, Hemiptera, and Acarina.

Among the Coleoptera, *Enoclerus sphegeus* Fab. was the most aggressive and responsible for the greatest predation. The small clerid, *Thanasimus undulatus* Say, was present in the area but rarely encountered. Dipterous predators included *Lonchaea corticis* Taylor, *Oscinella* sp. nr. *magnipalpus* Beck. and *Medeterus modestus* Van Duzee. A hemipterous egg predator, *Anthocoris musculus* Fall. was found occasionally within the main *Ips* galleries.

Two species of Acarina were found associated with the bark-beetle broods. An egg predator, *Pygmephorus* sp. was very common. The other species, *Uropoda fallax* Vitz. was less common. This paper deals principally with *E. sphegeus* and the two species of mites.

Coleoptera

Enoclerus sphegeus is abundant throughout the coniferous forests of western North America and is considered to be one of the more important predators of Scolytidae. It has been reported feeding on *Dendroctonus ponderosae* Hopk. (Böving and Champlain, 1920), *D. pseudotsugae* Hopk. and *D. monticolae* Hopk. (Chamberlin, 1939), and *Scolytus ventralis* Lec. (Struble, 1931). Within the experimental area in the foothills of Alberta, its main hosts were *Ips pini* and *Ips perroti*.

Champlain (Böving and Champlain, 1920) has given a brief outline of the behaviour of *E. sphegeus* in Colorado. Struble (1942) reported on its biology in the central Sierra Nevada region of California.

Methods

The abundance of this species and the ease with which it could be handled simplified field and laboratory observations. Eggs were obtained from infested slash and from field-collected females. Larvae in various stadia were reared in petri dishes. The larvae were placed between disks of dry white blotting paper and supplied with immature bark-beetle forms as required.

Adult

A search of the literature failed to reveal an adequate description of the adult (Fig. 11). On request of the author, W. J. Brown of the Systematic Entomology Unit in Ottawa kindly supplied the description which is presented below.

"Length 8.5 to 12 mm. Moderately slender. Abdomen bright red, the integument otherwise entirely blackish and with a feeble metallic lustre. Entire body conspicuously pubescent; the pubescence black and cinereous, erect in part; the cinereous hairs conspicuous on the head and legs, forming a conspicuous median band on the elytra; the band with irregular margins, slightly to moderately widened from the lateral margin to the suture. Antennae not quite attaining the base of the elytra, each with a club of four segments. Prothorax strongly narrowed in basal half; at base about three-fourths as wide as at apex; a distinct,

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arcuate, transverse impression extending completely across the apical half of the pronotum. Elytra feebly widened from base to apical third; with prominent humeral umbones; lacking striae; roughened by close, fine punctures. *E. sphegeus* differs from its allies by the relatively large size, the entirely blackish dorsum, and by the form and median position of the elytral band. It resembles closely only *E. moestus* Klug, in which the elytral band is postmedian and is strongly and abruptly widened near the suture. *E. moestus* Klug occurs in British Columbia".

Eggs

The eggs are 2.0 to 2.6 mm. in length and 0.6 to 0.8 mm. in width. At first they are salmon pink but white portions appear as the embryo reaches maturity. Eggs were laid under bark scales, at the entrance to the bark beetle gallery, or in boring dust at the entry hole. They were attached by one end to the bark, well protected from direct solar radiation and from predators. Eggs secured from captured specimens hatched in 19 to 22 days. This hatching period would probably have been considerably less, had the eggs been subjected to bark temperatures rather than the air temperatures existing within the laboratory tent where they were incubated.

Larvae

General—There are four instars. Head-capsule widths and total lengths are shown in Table 1. Struble (1942) reported only three instars but the four described here have been observed to occur.

Comparisons of fourth-instar larvae with a description of a "mature" larva by Böving (Böving and Champlain, 1920) agree in the important characteristics. Fourth-instar larvae can be readily identified through the use of the key provided by Böving.

Examination of the four instars reveals very few morphological characters peculiar to any stadium. Setae are more abundant on the third and fourth-instar larvae than on first and second. Setal length does not vary significantly between stages. Setal patterns, except for the head, do not appear consistent. The first and fourth instars, with setal arrangement, are illustrated in Figs. 1 and 10. The instars can be separated, however, using a combination of several somewhat gross morphological features i.e. size, cerci, colour. A summary of these characteristics is presented in Table 1. The first and second instars are easily separated. The third and fourth instars are so much alike in respect to setal pattern and setal abundance, structure and size, that separation is more difficult. Separation of these two latter instars is dependent on characteristics of the ninth segment and body colour.

Sclerotized portions of the larva i.e. head, dorsal thoracic plates, basal plate and cerci, are shiny brown. The colour is intensified towards the end of each stadium. The head of the full grown larva is very dark brown to black. The prothoracic shield is dark brown. The meso- and metathoracic plates and basal plate of 9th segment are lighter brown. The cerci are similar in colour to the head.

First Instar—(Table 1, Figs. 1, 2, 3). Larvae remained in this stadium from 7 to 14 days, although one larva moulted to second instar after two days but died soon after. It had not fed previous to moulting. The first-instar larva is very feeble, and when eggs are deposited any distance from a bark-beetle entry hole, it is improbable that the larvae are able to locate and enter before being destroyed by other predators, high bark temperatures, or starvation. In experimental

TABLE I
Features distinguishing larval instars of *Enoclerus sphegeus*

Instar	No. Measurements	Range in H.C. Widths mm.	Max. Length mm.	Distinguishing Characteristics of 9th Segment	Colour of body parts
I	4	0.51-0.55	7	See Fig. 2, 3. Basal plate not well defined Setae up to 3 times length of cerci. Cerci only slightly directed upwards, markedly divergent at apex. Apex not recurved.	Neutral white.
II	10	0.56-0.66	21	See Fig. 4, 5. Basal plate well defined Setae length of basal plate Cerci distinctly directed upwards. Base of cerci partially fused in dorsal appearance. Apex contracted, sharply recurved.	Initially white, having a slight pink cast when full grown.
III	12	1.00-1.40	23	See Fig. 6, 7. Basal plate well defined Setae approximate length of basal plate. Cerci directed upwards, parallel, widely separated. Apex slightly recurved, turned slightly inwards.	Light pink initially, to reddish cast when full grown.
IV	6	1.37-1.41	24	See Fig. 8, 9. Basal plate well defined Setae approximate length of basal plate. Cerci directed upwards, more so than III instar. Cerci sub-parallel, not widely separated at base. Apex recurved, strongly turned inwards.	Pink initially to purplish cast when full grown.

rearing this instar was able to attack successfully only first-instar or early second-instar *Ips* larvae.

Second Instar—(Table 1, Figs. 4, 5). The greatest predation of bark beetle larvae and pupae occurred in this stadium. In laboratory rearings, larvae remained in this stage up to 35 days. A single specimen, reared to check the number of instars, consumed 35 *Ips* larvae and pupae.

During the latter part of this stadium, larvae ceased to feed and remained stationary for periods up to 4 or 5 days. The body at this time was very turgid in appearance. The total length was about 3 times that of the first instar.

The difference in head-capsule size, between the second and third instar, warrants a more detailed description. The prothoracic segment commences to swell soon after feeding activity ceases, and prior to moulting is nearly as long as the mesothorax and metathorax combined and of much greater diameter than either. The rapidly developing third-instar cranium cannot be contained within the second-instar head capsule, and being unable to expand laterally, pushes back into the prothorax. This progressive elongation can be followed by observing the backward migration of the ocelli, visible through the second-instar head

capsule. There are five ocelli on each side of the head. The moulting has been observed many times. Prior to moulting the third-instar ocelli are visible near the extreme posterior rim of the second-instar head capsule, or anterior in the prothoracic segment. The second-instar head capsule contains the mouth parts, clypeus, and a portion of the frons of the third-instar larva. The second-instar prothoracic segment contains the remaining portion of the third-instar cranium. The cervix most commonly ruptures first, at the junction with the head capsule. The rest of the exuviae may be completely shed before the head capsule shows any rupture, and larvae may take several hours to shed this. The head capsule finally splits either along the epicranial suture and down one frontal suture and ventrally adjacent to the gula, (as defined by Snodgrass, 1935) or in both areas. Immediately following release from the old capsule, the extensively invaginated head of the third-instar larva undergoes rapid expansion. Full size is commonly attained in less than five minutes. The head, thoracic plates, and cerci are well coloured within 36 hours.

Third Instar—(Table 1, Figs. 6, 7). Reared specimens remained in this stage 7 to 14 days. Mature larvae and pupae were preferred, but teneral adult *Ips* were also successfully attacked. Within the experimental area, third-instar larvae were more common in late August and early September, when the bark-beetle broods were rapidly approaching maturity. The food supply for these, as well as the fourth-instar larvae, may become critical if the bark beetles begin to leave the galleries. A specimen in the third instar destroyed from 6 to 10 teneral bark beetles.

Fourth Instar—(Table 1, Figs. 8, 9, 10). Mature bark beetles were destroyed within the galleries by fourth-instar larvae. Large buprestid and cerambycid larvae in the vicinity of the bark-beetle broods were also destroyed. Although this was a very active stage in the development, food was frequently scarce and the larvae could apparently go for some time without feeding. One larva pupated and emerged successfully after having fed on only four teneral *Ips* in the fall.

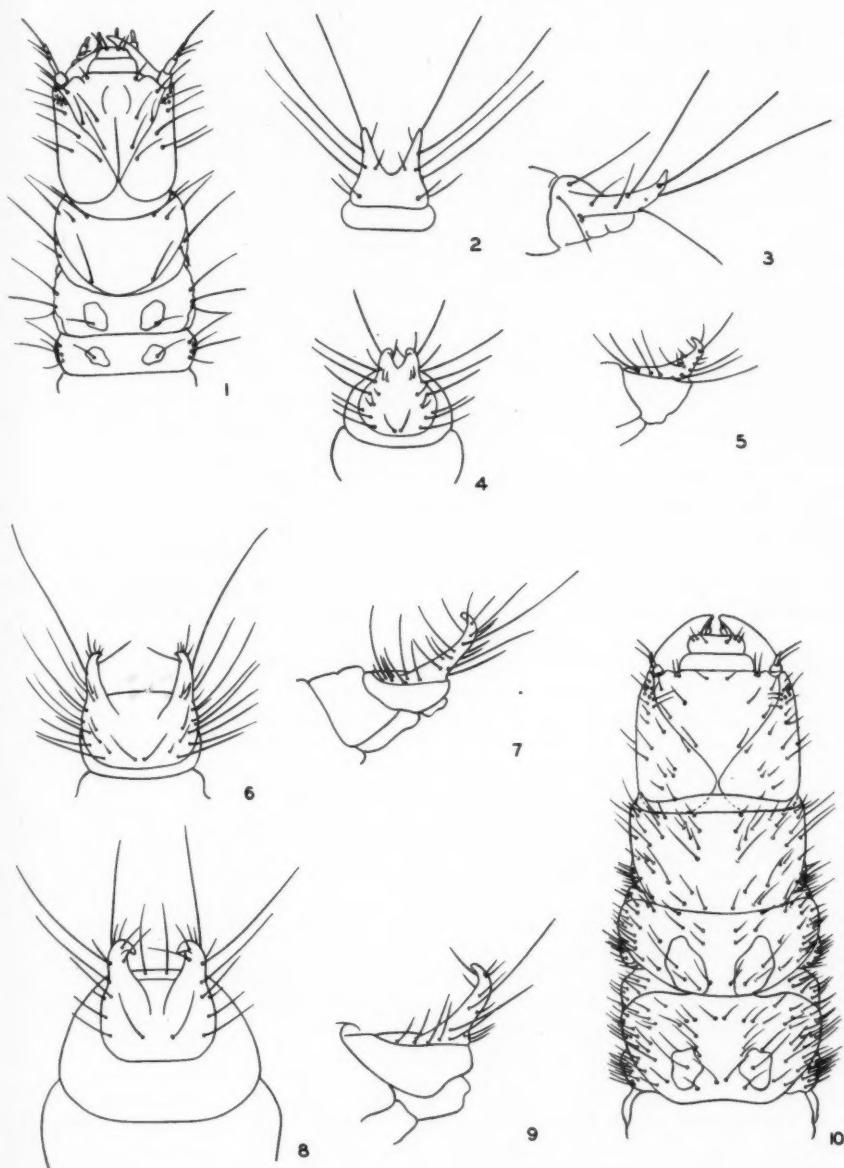
With the advent of cool fall weather, the fourth-instar larvae left the bark-beetle galleries and dropped into the duff, overwintering there in the larval stage. Cocoons were spun in the spring. Champlain (Böving and Champlain, 1920) recorded similar habits in Colorado. Reared specimens commenced construction of cocoons 20 days after being brought into room temperature. Food in the form of teneral and mature *Ips* adults was available to these larvae but they did not feed. The prepupal period lasted from 10 to 12 days within the cocoon.

Pupae

The pupal period lasted from 15 to 20 days. Fully coloured adults remained within the cocoons for periods up to 7 days before emerging.

Larval Habits

A single *Enoclerus* larva which was reared from egg to fourth instar was fed to satiation and a total of 40 *Ips* larvae, pupae, and adults were consumed. Observation on the larval feeding habits, in the field and in the laboratory, indicated a decided preference for *Ips* larvae and pupae, even when hymenopterous and dipterous larvae were common. Several second-, third- and fourth-instar *Enoclerus* larvae were placed in direct contact with larvae of Hymenoptera and Diptera. In all cases the predator, even when partially starved, showed a decided aversion to consuming these smaller forms. All the clerid larvae were reared on *Ips* larvae. Some cannibalism was noted in the third and fourth instars when larvae were overcrowded.



Figs. 1-10. *Enoclerus sphegeus* larva. 1, Instar I, head and thorax (X36). 2, Instar I, 9th segment, dorsal view (X36). 3, Instar I, 9th segment, lateral view (X36). 4, Instar II, 9th segment, dorsal view (X18). 5, Instar II, 9th segment, lateral view (X18). 6, Instar III, 9th segment, dorsal view (X18). 7, Instar III, 9th segment, lateral view (X18). 8, Instar IV, 9th segment, dorsal view (X18). 9, Instar IV, 9th segment, lateral view (X18). 10, Instar IV, head and thorax (X18).

An *Enoclerus* larva moved through the galleries with its hypognathous head lowered. When attacking its host, the predator thrust its opened mandibles upwards, and punctured the ventral or lateral surface. The head was forced progressively farther into the victim, and the mandibles could be seen working in a raking fashion, forcing the body contents of the host towards the oral cavity of the predator (Fig. 12). Clerid larvae had difficulty in attacking unless the host was confined within a small space which allowed the predator bracing and leverage action. The third- and fourth-instar larvae were unable to destroy adult bark beetles unless the host was within the gallery.

Adult Habits

A freshly cut lodgepole pine was kept under observation in the spring. Three weeks later, on June 12, *Ips* attacked this tree "en masse" in midafternoon of a warm sunny day. The following day a number of *Enoclerus* adults were observed moving over the bark, feeding heavily on the bark beetles. Adult *Ips* with only the posterior projecting from entry holes were commonly pulled out and consumed by the predator. There was considerable predation by *Enoclerus* adults before the attacking bark-beetles managed to establish themselves under the bark.

During this period females of *Enoclerus* were observed laying eggs under bark scales. The males were very aggressive during mating, and several males might keep a female occupied for periods up to five minutes before she was able to escape. Oviposition was observed four to five minutes after copulation. Frequently the female moved about ejecting and retracting the ovipositor but laying no eggs, possibly seeking a satisfactory site.

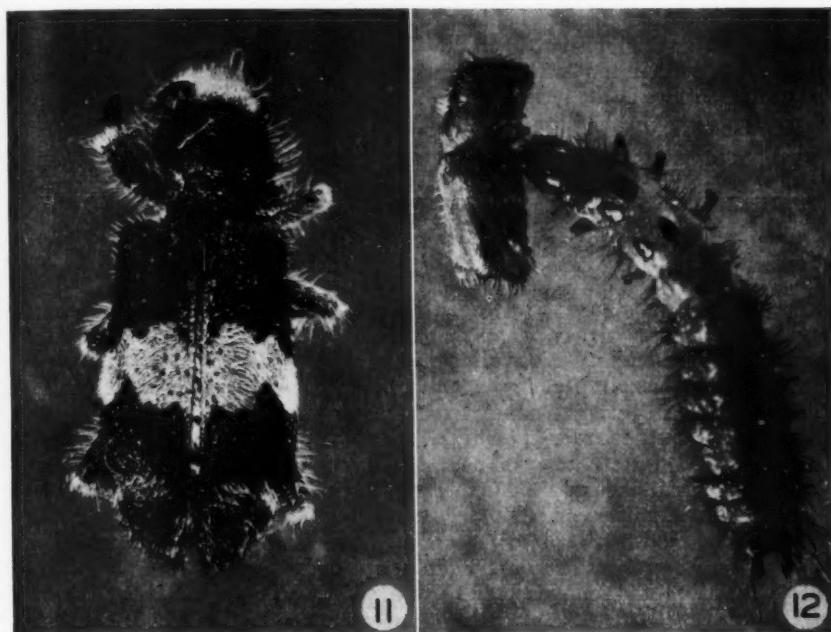
Females kept under observation in petri dishes were reluctant to lay eggs, possibly because of the absence of essential environmental stimuli. After a period of several days they deposited a few eggs at random over the bottom of the container or within folds of the cloth covering the bottom. In several cases, males consumed these eggs before they could be taken out. The largest number of eggs laid in a petri dish by a single female was six. Struble (1942) reports that in laboratory tests females laid from 5 to 93 eggs.

The absence of adults from bark-beetle infested slash was very noticeable once the adult bark beetles became inaccessible by boring beneath the bark. Within a week or so of the disappearance of adult bark beetles, there was little evidence of *Enoclerus*. It seems probable that most of the adults die of starvation, once the bark-beetle adults are no longer available. The larvae require an abundance of food and this can only be obtained in brood galleries containing an accessible and continuous source of immature bark beetles. In addition, the development of the predacious larvae must parallel closely the development of the host. It is essential that very young bark-beetle larvae be available as food for the first-instar *Enoclerus* larvae.

Acarina

Two species of mites were commonly found in galleries of *Ips pini* and *Ips perroti*. One of these, *Pygmephorus* sp. (Pyemotidae) is an egg predator. Available evidence indicates that the other species *Uropoda fallax* Vitz. (Uropodidae) is predacious on *Pygmephorus* and other small organisms common in the main galleries of the bark beetles.

A short review of the association between mites and scolytid was given by Chamberlin (1939). A number of references were quoted. The role of mites as an agency of natural control of the Douglas fir bark beetle was recently illustrated by Walters and Campbell (1955).



Figs. 11-12. 11, *Enoclerus sphegeus* adult. 12, Third-instar larva attacking *Ips pini* teneral adult.

Pygmephorus sp.

This mite was the most important egg predator found in this study. No figures are available on abundance but its presence was noted in approximately 60 per cent of the slash samples. In selected galleries examined under magnification it was not uncommon to find as many as 33 per cent of the bark-beetle eggs with mites attached.

Adults of *Pygmephorus* sp. are minute, flat, white, or translucent and average 0.118 mm. in length. Adults were carried into the bark-beetle galleries, during the spring and summer flights, on the ventral surface of the adult beetles. Once in the gallery, they released themselves from the beetle and females forced their way past the egg plug, attaching themselves to the newly laid bark-beetle eggs. The females then began to swell, and eggs became visible within their bodies. Sometimes a dozen eggs were extruded while the female was expanding. She became spherical in shape and reached a diameter of 0.356 mm. The body was densely packed with eggs which were clearly visible through the body wall. The mites remained alive but completely immobile. An egg mass, gravid female, and host egg removed from an *Ips pini* egg niche are illustrated in Fig. 13. The bulk of the eggs were released when the body of the mite ruptured but most of the eggs remained in situ. As many as 30 eggs have been counted in one egg mass.

The eggs hatched within seven days. The bark-beetle egg was punctured by the newly emerged mites and in a short time the egg was deflated. Young mites then moved into the main galleries where they were common throughout the summer but their food during this period is not known. No evidence of

attack on bark-beetle larvae could be found. When the *Ips* brood matured and adults began moving under the bark, the mites attached themselves by embedding their mouth parts in the beetles. They were found most commonly attached to the ventral surface at the junction between head and thorax, and around the base of the legs (Fig. 14). Mites left the gallery with the beetle and overwintered attached to the beetle in the duff. The following spring they were carried to fresh galleries and the cycle was repeated.

Uropoda fallax Vitz.

These brown disk-shaped mites were less abundant than the preceding species but still common. They measure 0.264 mm. by 0.396 mm. and are heavily sclerotized.

Their relatively large size tended to reduce their effectiveness as egg or larval predators since they were unable to work their way past a normally compact egg-niche plug. No sign of predation on *Ips* by this mite was revealed during the examination of a large number of egg galleries. They were observed feeding on exposed newly hatched *Pygmephorus*, as illustrated in Fig. 15. The egg-niche plug had been loosened in the course of examining an adjacent area of bark. Probably these mites would feed on bark-beetle eggs, larvae, and pupae if the opportunity occurred.

In the late summer and fall, *U. fallax* adults attached themselves by embedding their mouth parts into the elytral declivity (Fig. 16) or membranous tissue on the ventral surface of the adult bark beetles. They overwintered on the *Ips* adults and the following spring were carried to new galleries in the same manner as *Pygmephorus* sp. It was not uncommon to find both species of mites attached to an overwintering adult.

Summary

At Strachan, Alberta, the most important predators of *Ips pini* Say and *Ips perroti* Sw. were the following:

Coleoptera—*Enoclerus sphegeus* Fab., *Thanasimus undulatus* Say.

Diptera—*Lonchaea corticis* Taylor, *Medeterus modestus* Van Duzee, *Oscinella* sp. near *magnipalpus* Beck.

Hemiptera—*Anthocoris musculus* Fall.

Acarina—*Pygmephorus* sp., *Uropoda fallax* Vitz.

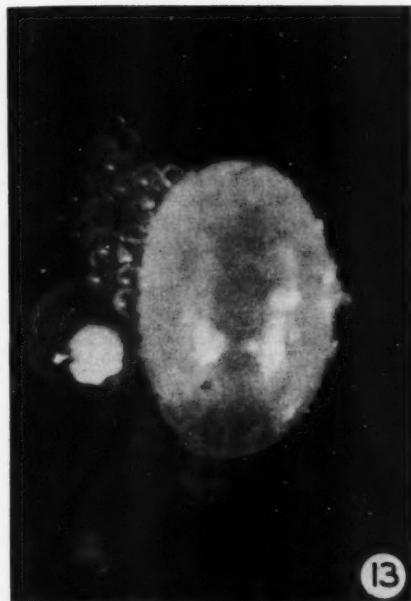
Only *E. sphegeus* and the mites were studied in any detail. The former laid eggs on the outside of slash infested by bark beetles. The young clerid larvae made their way into the bark beetle galleries. There were four instars which fed on the various bark beetle stages. Mature larvae left the slash in the fall and hibernated in the duff. Adults emerged in the following spring. Descriptions of the adult and larva are given together with notes on their behaviour.

The mite, *Pygmephorus* sp. was carried into the bark beetle galleries attached to the ventral surface of the host. It then detached from the host and laid as many as 30 eggs which hatched within 7 days. The young mites fed on bark beetle eggs and when full grown attached themselves to beetles of the new brood, leaving the gallery and overwintering on the host in the duff.

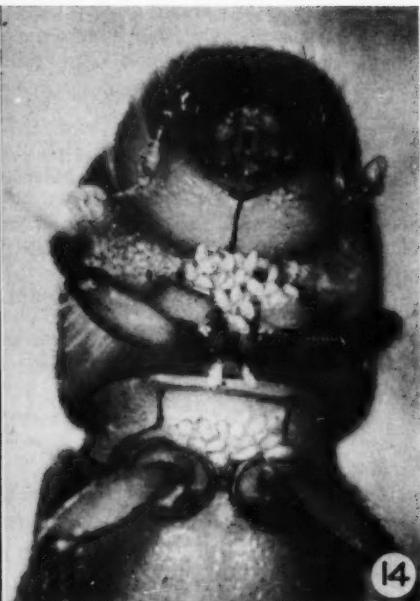
U. fallax attached itself in the elytral declivity or on the venter of the host. It overwintered on the beetle and was carried to new galleries in the same manner as *Pygmephorus* upon which it was seen to feed. It does not appear to be very effective as a bark beetle predator.

Acknowledgments

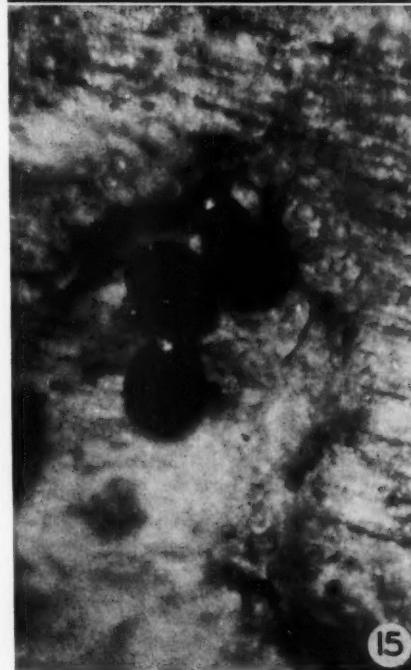
The assistance of various members of the Calgary Forest Zoology Laboratory during the preparation of this manuscript, is gratefully acknowledged.



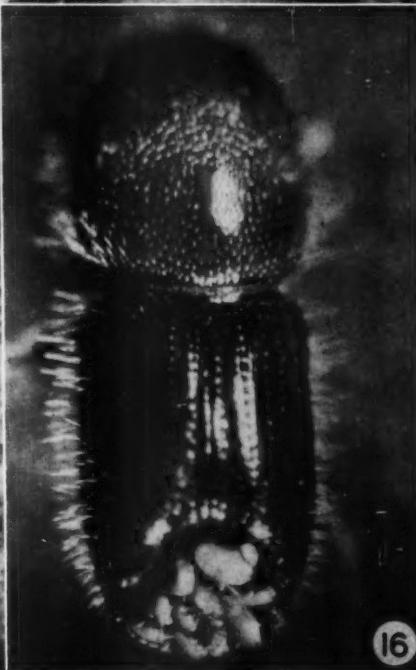
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Figs. 13-16. 13, *Pygmyphorus* sp. Gravid female with egg mass on egg of *Ips pini*. 14, *Pygmyphorus* sp. on venter of *Ips pini*. 15, *Uropoda fallax* feeding on newly hatched *Pygmyphorus* sp. 16, *Uropoda fallax* on elytral declivity of *Ips pini*.

Thanks are extended to members of the Systematic Entomology Unit in Ottawa for identifying the insects. Appreciation is expressed to Dr. H. H. J. Nesbitt, of Carleton College, Ottawa, for identifying the mites.

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Physical Environment and Behaviour of Immature Stages of *Aedes communis* (Deg.) (Diptera: Culicidae) in Subarctic Canada¹

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Introduction

Studies on the biology and control of biting flies in the Canadian north have been described by Hocking *et al.* (1950), Twinn *et al.* (1948), and Twinn (1950). The biological investigations have been directed largely toward the economic control of biting flies in isolated military areas. In the subarctic regions of North America so many factors influence the rate of development of mosquitoes that simple relations of time and temperature cannot be used to estimate adequately the periods of infestation. Casual field observations of mosquito larvae and pupae suggested that behaviour patterns peculiar to northern species modify the effect of environmental conditions on the rate of development.

This paper is a report on observations of the behaviour of immature stages of *Aedes communis* (Deg.) at Fort Churchill, Manitoba, from 1950 to 1952. *A. communis* was selected as the best species for study for the following reasons: (a) It was the most abundant species that occurred alone in the larval stage in pools in the locality. (b) Unlike other species, it occurred by itself in certain types of pools in semi-forested areas, so that identifying populations was simpler. (c) The behaviour of the immature stages did not appear to be fundamentally different from that of other pest species of *Aedes* when comparisons were made in the same locality.

Description of the Area

Topography

The site for the studies was approximately 12 miles south of Churchill on a portion of low muskeg between Warkworth and Goose creeks near their conflu-

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ence with the Churchill River. The subsoil consisted of a varying composition of gravel, sand, humus, and boulders. The area under direct observation was very near the transition between the Precambrian and the Ordovician formations and within the Trenton limestone deposits characterizing the latter formation south of Churchill.

The general area was low, level muskeg traversed by a network of shallow, branching, and anastomosing streams and creeks. Pools were very numerous and varied in size and depth. They were mainly shallow with sloping banks and muddy borders and bottoms in the open, boggy portions of the muskeg; but near the water courses they were deep and quasi-permanent with steep, high banks held firm by vegetation.

Vegetation

The study site was approximately in the centre of an area 600 yards wide bounded on the north and south respectively by Warkworth and Goose creeks. The vegetation was typical of the transition between the Boreal forest and tundra regions. A sparse stand of scrub spruce (*Picea* sp.) covered the area between the two creeks. The large, deep pools of the type used to study mosquito behaviour frequently contained a growth of grass (*Poa* spp.) and sedge (*Eriophorum* spp.) at their borders and thick mats of mosses and phanerogams (principally *Hippuris* spp.) below the surface of the water near the peripheries. Most of the growth of the submerged mosses occurred in late summer after the mosquitoes had emerged, by which time the water level in even the large pools was low. The pools were usually surrounded by thick hummocks of willow (*Salix* spp.), *Vaccinium* spp., or *Ledum groenlandicum*, thickly matted at the bases by mosses. The hummocks provided the firm, vertical banks that were characteristic of the large, deep pools in the locality. Bottoms of quasi-permanent pools usually contained no vegetation on the mud, especially near the centres; but in pools of more temporary nature the bottom mud was often covered by *Carex* or *Eriophorum* spp. Ordinarily the vegetation provided no permanent shade for the pools in which *A. communis* bred.

Climate

The study site was within the permafrost area, which includes the tundra region and extends south through the Transition zone to the Boreal forest region. Except where the soil lacks the usual surface vegetation of mosses and lichens, the permafrost does not thaw more than six inches below the surface in a normal summer. The permafrost probably keeps deep pools permanent or quasi-permanent, particularly in drier periods during spring and summer. The permafrost replenishes at least in part the water lost when precipitation is light. It also helps to contain the water by preventing seepage through the bottom mud to surrounding terrain. Occasionally, large, shallow pools that maintained a fairly constant water level over a period of weeks drained almost completely within two or three days when the permafrost receded low enough in one of the banks to allow the water to drain off into lower pools or streams.

Apparently the melting of the permafrost under the surface mosses was influenced more by warm rain than by any other meteorological factor. The sudden disappearance of pools was usually observed to occur during or soon after heavy falls of warm rain. Therefore the fall in water level in permafrost areas was not completely dependent on a combination of increased evaporation and reduced precipitation.

The weather was characteristically variable even during the summer months. Table I indicates that temperatures were below normal in 1950 and above normal

TABLE I
Temperature, precipitation, and sunshine recorded at Fort Churchill, Manitoba,
May-August, 1950-1952 by the Aviation weather office

Year	Month	Temperature, °F.				Sunshine, hr.	Total precipitation, in.	Snowfall, in.
		Max.	Min.	Mean	Normal mean			
1950	May	68	8	28	30	158	2.2	4.5
	June	76	26	38	42	154	0.8	traces
	July	81	36	52	53	318	0.6	-
	Aug.	85	33	51	52	238	3.8	-
	Average	78	26	42	44	217	1.85	
1951	May	55	15	31	30	125	3.1	traces
	June	81	19	45	42	249	0.4	-
	July	85	38	52	53	317	0.8	-
	Aug.	83	39	57	52	264	1.3	-
	Average	76	28	46	44	239	1.40	
1952	May	69	24	34	30	158	1.3	traces
	June	84	28	45	42	262	1.8	-
	July	84	33	50	53	276	1.5	-
	Aug.	77	38	51	52	218	4.1	-
	Average	78	31	45	44	228	2.18	

in 1951 and 1952. The annual climax of normal daily temperatures based on all the temperature records available for Fort Churchill is 56°F. and it occurs between July 23 and August 1.

General Methods

The behaviour of *A. communis* larvae and pupae was studied in detail in relation to the daily rhythm of diurnal warming and nocturnal cooling in natural pools. The observations were confined mainly to two pools, A and B, in a sparsely wooded area of scrub spruce and scattered willow. These pools were among the larger of those in which the species usually breeds; 8 to 12 feet in diameter and up to 20 inches in depth. As they were deep and had almost vertical banks, the peripheral contours remained regular during most of the developmental period of the mosquito irrespective of fluctuating water level. Pool A had the greater depth, the larger mass of ice and permafrost, and less spruce cover near its borders. Since meteorological factors had free play with a minimum of interference from forest cover, pool A was not only the more suitable for observing the movements of larvae and pupae but also more nearly an average mosquito pool in the transition area between forest and tundra. Pool B was sheltered more than usual by scrub spruce; the surrounding trees interfered irregularly with the effects of such meteorological factors as solar radiation and wind. This pool was selected especially to check the effect of forest cover on mosquito behaviour.

Both pools were marked off with 18-inch grids. The grids were heavy cords strung between pegs on opposite banks and pulled taut just above the surface of the water (Fig. 1). The movements of aggregations of larvae and pupae, the location of temperature-reading points, and significant daily changes in the character of the pool were recorded by reference to the grid system.

Temperatures in the pools were recorded with a potentiometer and copper-constantan thermocouples (Fig. 1, a-c). Twelve thermocouples were suspended by lead wires above the grid system. Ten of these were mounted securely to

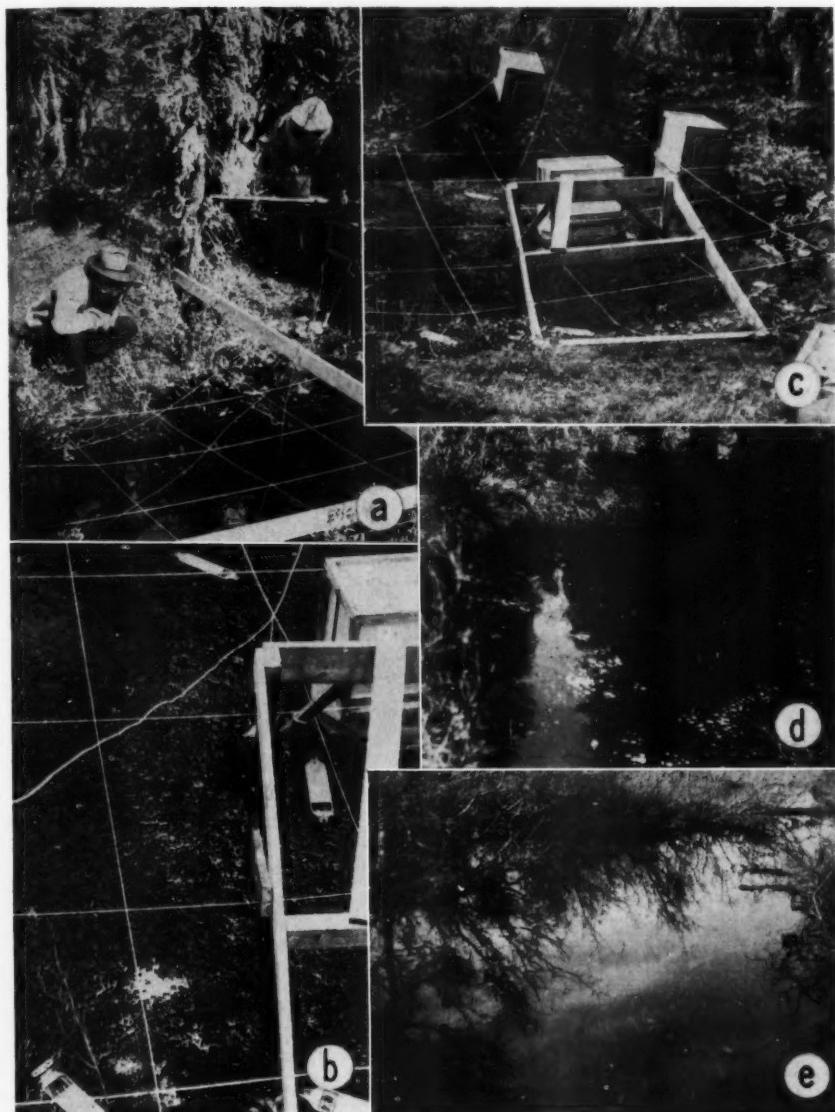


Fig. 1. Mosquito pools at Fort Churchill, Manitoba: (a) A portion of pool A showing the grid system and arrangement of thermocouples and potentiometer. (b) A portion of pool B after the mosquito adults had emerged, showing (i) the copious growth of moss after permafrost receded from the bottom of the pool and (ii) the distribution of thermometers used to give the maxima and minima of horizontal gradients. (c) View of pool B with cages after the completion of emergence, showing the vertical banks that indicate the depth of the pool when full at the beginning of the season. The ramp permitted access to the middle of the pool without disturbing the bottom. (d) The type of pool usually found in scrub forest in transition between Boreal forest and tundra. (e) Pool with irregular willow-covered borders commonly found near water courses.

measure the temperature of the water one inch below the surface. Henceforth in this paper the term *one-inch temperature* means the temperature of the water one inch below the surface of the pool. The remaining two thermocouples were mounted directly below a one-inch thermocouple at the centre of the pool, one at four and the other at eight inches below the surface. The layers of water below eight inches were so cold by comparison with the water above that larvae were observed to seek temperatures below that depth only when surface temperatures were below 39°F. Therefore three thermocouples in a perpendicular plane at the centre of the pool were sufficient to indicate changes in the vertical temperature gradient in the water in relation to behaviour; the other ten indicated the horizontal temperature gradients. All the thermocouples were connected to the potentiometer by leads through a multiple contact switch. This arrangement permitted the whole series of temperatures in the pool to be recorded as simultaneously as possible without disturbing the water.

A complete set of temperatures was recorded on the hour every two hours each day during daylight. At the same time the positions and depths of aggregations of mosquito larvae and pupae in relation to micro-environmental temperatures were observed and recorded. The temperature at the centre of each aggregation was recorded with a portable thermocouple attached to a long flexible lead wire and supported on a light pole long enough to reach any part of the pool. A portable thermocouple with graduated lead was also used occasionally to measure the temperature of water within aggregations at depths below eight inches when exceptional behaviour was observed.

Weather conditions were recorded on the spot for each observation of mosquito behaviour. Solar radiation was measured with a General Electric radiation meter calibrated in gm.-cal./cm.²/min. Weather changes were recorded in detail and related to changes in the characteristics of the pool. The thawing of pool banks and the recession of ice and permafrost from the pool bottom were carefully observed from day to day. The significance of these changes in relation to the thermal conditions in the pool was recorded. Additional records of air temperature, humidity, cloudiness, rainfall, and other synoptic weather information were available from continuously recording instruments at the field laboratory within 300 yards of the study site or at a meteorological station 10 miles away.

There were large populations of larvae in both pools. The numbers were estimated on an overcast, calm day when there was random distribution. Counts were made above a galvanized tin plate placed at various places on the bottom of each pool. The total population of each pool was estimated as the product of the average count of larvae per unit area and the total area of the pool. The estimate, made when most of the larvae were in the second instar, exceeded 20,000 in pool A and 14,000 in pool B. The populations remained at approximately these levels during the investigation, predators being few.

Relation between Meteorological Factors and Thermal Variations in Mosquito Pools

The environment of mosquito larvae and pupae in a pool is constantly subjected to a combination of meteorological and edaphic factors. The meteorological factors normally change continuously and suddenly, whereas the edaphic factors, although under the influence of meteorological phenomena, normally vary more slowly. As compared with some gradual and relatively small-range variations that have been described for mosquito environments under forest canopy in temperate and tropical regions (Boyd, 1929; Missiroli, 1935), both

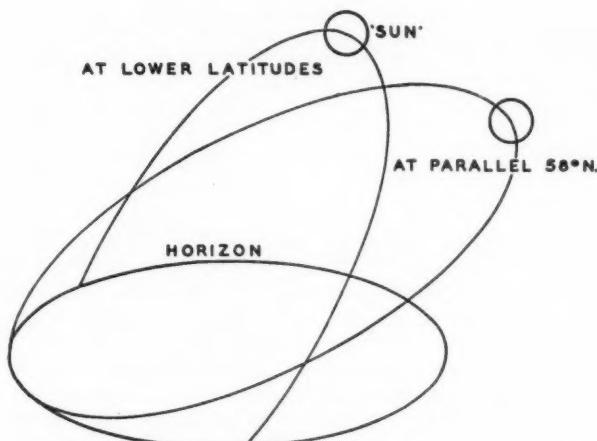


Fig. 2. A comparison of the angle of inclination of the sun's rays to the horizontal at parallel 58°N. and at lower latitudes at the same time of year.

daily and seasonal meteorological conditions influencing pools in far northern areas are subjected to abrupt and extreme changes. Edaphic factors under these circumstances become a significant regulating influence on the thermal conditions of a pool.

During the winter, the pools were frozen throughout and pool ice became continuous with the underlying permafrost. In the spring, thawing began along their mossy borders and progressed gradually downward and toward the centres unless the surrounding vegetation caused the insolation to be very irregular. Once the ice became free from the banks, thawing at the surface was rapid; but, especially in the middles of the pools, where the thermal effect of solar radiation was reduced with depth, continuous contact with the permafrost caused the bottom ice to melt slowly. In the larger pools comparable to the two selected, the permafrost maintained this regulating influence on the temperature of the pool during most of the developmental period of the mosquito. In a normal³ year the permafrost receded below the surface of the bottom mud of most pools at the beginning of the pupal period; in exceptionally deep pools the permafrost maintained contact with the water at the centre for considerably longer periods.

Many of the eggs of northern species of *Aedes* are laid along the grassy or mossy margins of pools. First-instar larvae that hatched at the periphery of a pool could develop near the bank under near-optimum conditions after early spring thaws. Usually first-instar larvae were abundant along the margins of pools before the surface ice had receded more than a foot from the bank. The maximum horizontal temperature gradient observed in marginal, open water in ice-covered pools was 32 to 46°F. at the surface. Second-instar larvae were usually abundant in a large pool before the ice had disappeared from the surface. As the surface ice receded, the maximum temperature gradient increased only slightly and was invariably steepest near vegetation on the bank. Apparently water at the high-temperature end of the gradient was warmed principally by the insolation of marginal vegetation and mud in shallow areas; scattered formations of ice increased both horizontal and vertical gradients.

³Based on the normal daily temperatures given by the Meteorological Service, Canada Department of Transport, for the Churchill, Manitoba, weather station.

TABLE II

The angles of the path of the sun's rays to the horizontal as the sun crossed the meridian at Fort Churchill (latitude 58° 43' N.) during studies in mosquito behaviour in June and July

Date		
June	1.....	53° 59'
	15.....	55° 18'
July	1.....	55° 9'
	15.....	53° 37'
	31.....	50° 24'

At high latitudes, the vertical and horizontal gradients in the temperature of a pool are intensified by solar radiation. At Fort Churchill (latitude 58° 43' N.) the path of the sun on reaching its zenith is closer to the horizon than it is at lower latitudes. The path of the sun's rays affects the temperature gradients in pools at higher as compared with lower latitudes (Fig. 2). Because of the angles that the path of the sun's rays make with the horizontal at Fort Churchill (Table II), especially in a small pool surrounded by vegetation, only a sector is insolated at any one time on a normally clear day. In the early forenoon, the centre of maximum heating in a pool was in an insolated sector on the southwest side. At sunset, this centre had moved clockwise with the sun around the periphery of the pool to the southeast side. Although the insolated sector increased considerably in area by noon, a centre of maximum heating was always maintained on a sunny day and a horizontal gradient of as much as 12°F. was observed between the southerly and northerly margins of pools free of surface ice for several days. Fig. 3 shows the relation between the source of insolation and the thermal gradients observed in pool A at 4.00 p.m. on July 1, 1951. This observation was made two hours after maximum insolation of the pool and indicates a horizontal gradient of 10°F. at the surface and a vertical gradient of 29°F. at the centre. The relation of the underlying permafrost to the pool and its banks is also shown in the figure.

Convection currents were observed in unequally insolated pools on clear, calm days when solar radiation was intense. By noon on a clear, calm day, a

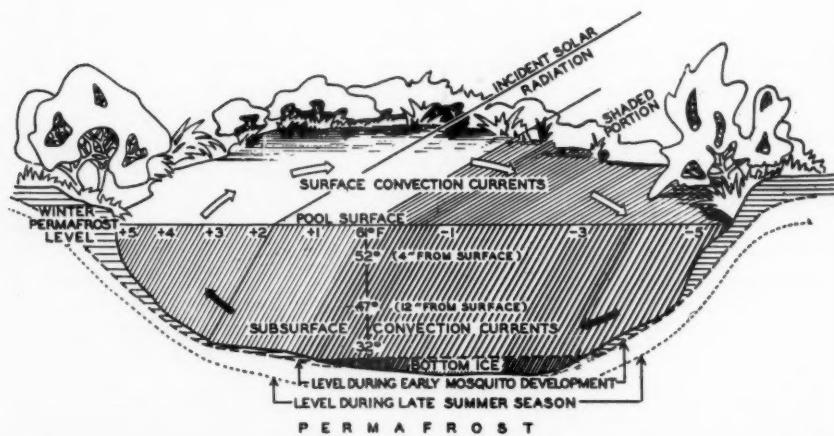


Fig. 3. Sectional drawing of a pool in perspective showing vertical and horizontal temperature gradients in relation to the source of insolation.

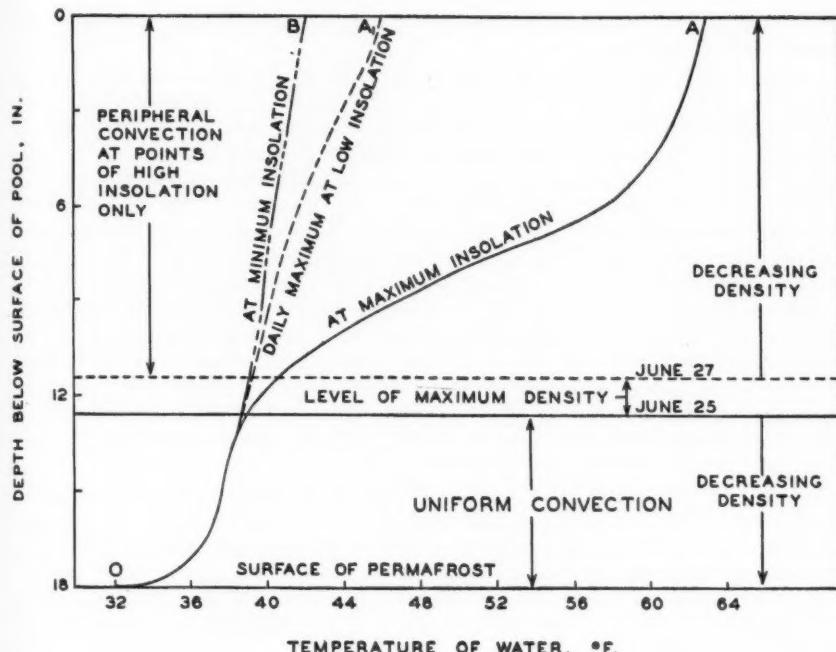


Fig. 4. Convection and limits of the daily vertical variation in temperature in a pool with subjacent permafrost. The curves OA and OB represent the maximum and minimum gradients of temperature on a sunny day, June 25, 1951. OA₁ represents the maximum gradient during heavy overcast two days later.

clockwise circulation could be observed at the surface of the water. This circulation was probably due to the water rising at the point of maximum heating and spreading over the surface. As previously indicated, temperature gradients were greater near clumps of moss and mud at the margins of the pools. Location of points of maximum heating within an isolated sector depended considerably on the presence of organic material capable of absorbing radiation, especially along the banks. The convection currents generally moved clockwise, probably under the influence of the clockwise movement of the isolated sector around the pool (Fig. 3). These currents were not observed when solar radiation had been low for the previous part of the day or when the maximum temperature of the water was relatively low. Under these conditions the range of vertical temperature gradients was 8°F. or less as compared with 31° during peak insolation on warm days. Although convection currents depending on density are theoretically possible in water with a vertical temperature gradient, they were imperceptible in pools with surface temperatures lower than 40°F. Therefore changes in density would promote little or no convection in a layer of water with a temperature of 32 to 39°F. directly above the bottom ice or permafrost in a pool. Hence the melting of ice or permafrost at the bottom of a pool was delayed by a nearly convection-free layer of water and, in the lowest levels of the pool, the rate of melting depended on insolation and the thermal conduction of the lowest water layer. Wind had little, if any, effect on the pattern of

circulation at the surface of the water since the protecting banks were high and covered with vegetation.

The daily variation of temperature with depth was studied in pool B during two days. One was a calm, warm day with intense solar radiation; the other was a calm, overcast day with a minimum of solar radiation. The vertical gradients were measured at the point of maximum heating at intervals of one hour throughout the day. The greatest vertical gradient observed under intense solar radiation is shown by the curve OA in Fig. 4 and that during very low solar radiation by the curve OA₁, the maximum temperature in the pool for the day being represented by the point A. The temperature at the top of the bottom ice (or permafrost) is represented by the point O. The minimum surface temperature in the pool for the day is represented by B and the curve OB shows the smallest vertical temperature gradient for the day. The temperature of the water at different levels in a pool with subjacent permafrost probably varies between limits, i.e., a maximum OA and a minimum OB, that depend on (i) the proximity of the permafrost, (ii) the depth of the pool, (iii) the maximum amount of insolation in the summer season, and (iv) the conductivity of the water and the air moving over the pool.

The general circulation in pools varied in degree under different weather conditions. When the sky was completely overcast, surface water was heated uniformly and horizontal temperature gradients disappeared. Clouds occasionally caused irregular insolation. Observations on a few pools with highly irregular contours indicated that convection patterns became complex when jutting banks obstructed either the movement of the water or the insolation of any part of the pool.

Behaviour of Larvae and Pupae in a Pool Exposed to Varying Insolation

A daily system of behaviour was observed for both the larvae and pupae of *A. communis*. It soon became evident in the regular daily observations that, except on rare occasions, there were not more than two aggregations in a pool at any one time. A slightly detached portion of one of the major aggregations occasionally appeared as a third and minor one. Correlation of the movements of the two normal aggregations with environmental conditions indicated the reasons for this behaviour. Invariably during the rise of the sun to its zenith on a clear day, one aggregation of larvae was found in the insolated sector of the pool at the point of maximum heating. This aggregation usually formed quickly and increased in numbers to its major proportion in the morning; thereafter it decreased slowly until dispersing in the evening. The second aggregation formed two to four hours after the first and remained in the shaded sector of the pool near the warmest part of the border of the insolated sector. The relative positions of the two aggregations were maintained throughout most of the day. As the first aggregation moved clockwise around the pool with the advance of the insolated sector, the second aggregation followed in the same general direction, maintaining its position in the shaded part of the pool close to the warmest, or trailing, border of the insolated sector. The positions of the two aggregations are shown in Fig. 5.

The first aggregation formed only when a sector of the pool was being more intensely insolated than the remainder and persisted until (a) the insolation was interrupted or (b) until the general surface temperature of the pool increased to more than 61 to 62°F. The second aggregation increased steadily in numbers throughout the day but dispersed suddenly (a) when the surface temperature in the wake of the insolated sector increased to 61°F. or (b) when the solar

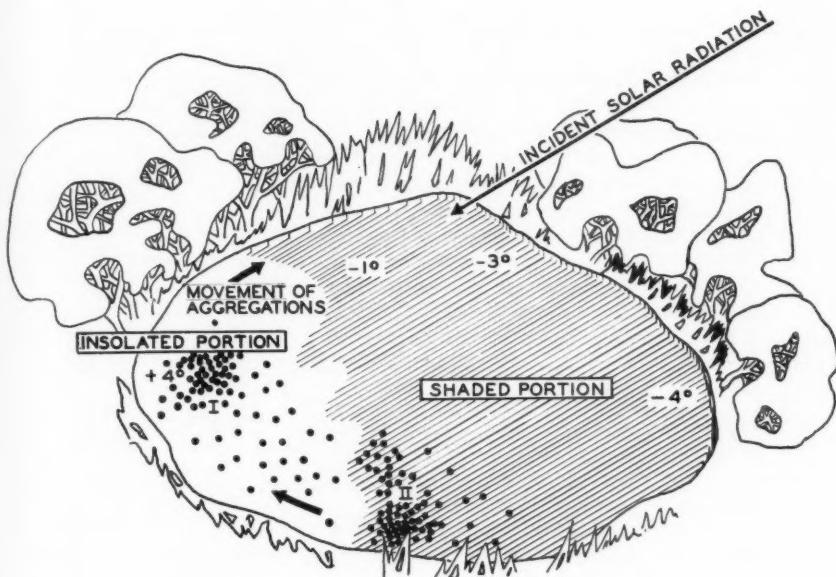
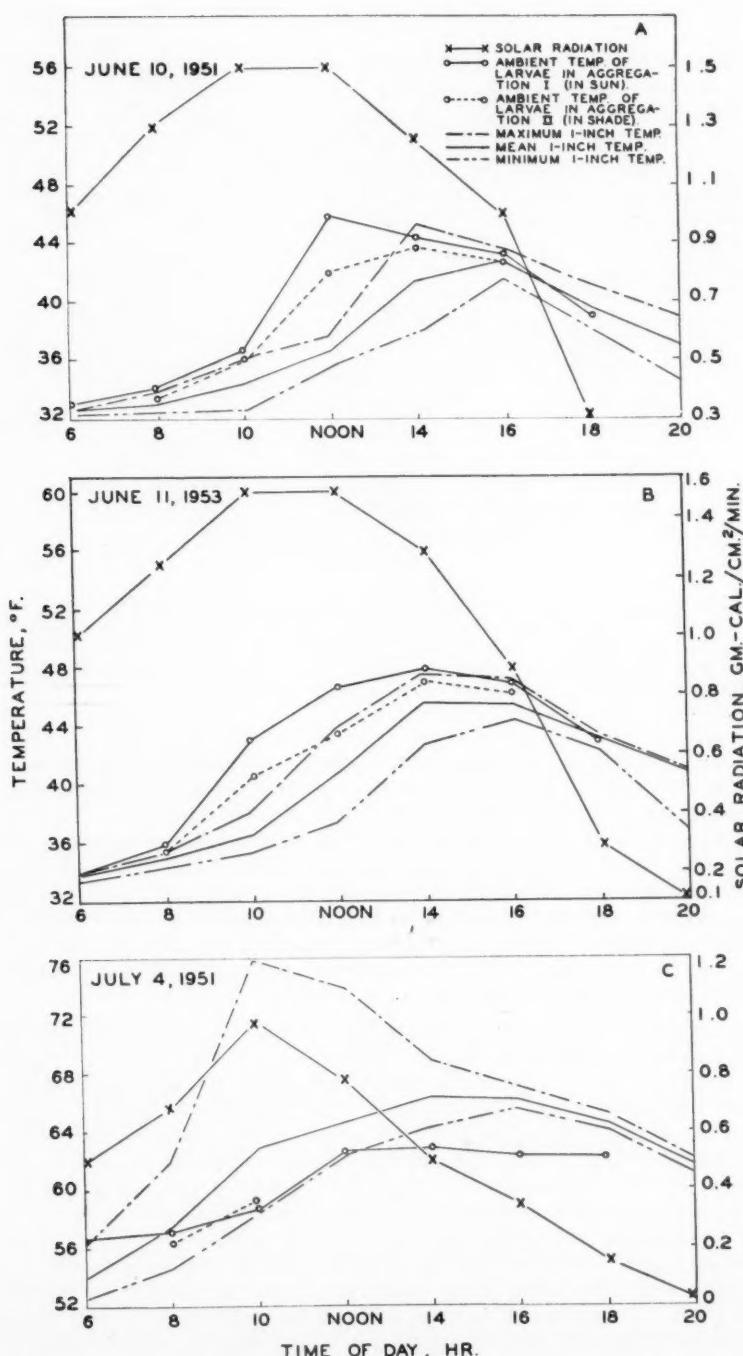


Fig. 5. Relation of insolation and gradients of temperature in a partially insolated pool to the disposition of aggregations of mosquito larvae. Arabic numerals indicate the differences between the temperatures at one inch below the surface and the mean for the pool at the same depth as recorded from a single set of observations. The arrows indicate the movement of the aggregations under the influence of the changing insolation.

radiation dropped in the afternoon to the point at which the surface temperature of the insolated sector of the pool became less than the surface temperature of the shaded water at its trailing border, i.e., after the horizontal temperature gradient at the surface ceased to exist and light intensity became uniform. The larvae in the second aggregation usually dispersed in the shaded sector of the pool about three hours after maximum insolation for the day, i.e., at 5 to 6 p.m. The first aggregation persisted much later and maintained its position within the insolated sector even when the ambient temperature of the aggregation was lower than 60°F. or lower than the surface temperature in shaded portions of the pool previously traversed by the sun's radiation.

The system of temperature selection by the larval aggregations for consecutive observations on individual days is shown in Fig. 6. Fig. 6, B is for a bright, warm, cloudless day. The regularity of movement of the aggregations in relation to regular changes in pool temperature is obvious. During increasing or high insolation, both aggregations remained within the upper half inch of water, thereby selecting temperatures higher than the maximum one-inch temperatures. As the solar radiation decreased in intensity in the evening, the larvae in the second aggregation dispersed when the temperature of the insolated sector of the pool became lower than that of previously insulated sectors. The first aggregation dispersed later when the intensity of solar radiation became very low, presumably when the larvae were no longer stimulated by radiation. Obviously on a bright, warm day with scattered cumulus clouds, the behaviour of the larvae (Fig. 6,A) was essentially the same as that on a clear, sunny day.



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(Fig. 6,B) except that there was a slight irregularity in the progression of temperature changes and in the disposition of the aggregations. On both these days the temperature in any part of the pool was less than 60°F. On a hot, calm, sunny day that became hazy in the latter part of the morning and eventually became overcast in late evening (Fig. 6,C) even the minimum one-inch temperatures of the pool were above 60°F. by noon, and the ambient temperatures of both aggregations were below the mean one-inch temperature. From 8 a.m. to the end of the day the major parts of the aggregations remained at a depth of several inches, only a small portion coming to the surface and working downward at any one time. The second aggregation persisted for only a small portion of the morning and dispersed when the mean one-inch temperature of the pool rose above 62°F. Apparently the first aggregation persisted throughout the day by working from the surface to lower depths to select preferred temperatures. The significance of these observations is discussed later.

No aggregations of larvae were observed on overcast days when solar radiation was low. When initially bright days became cloudy, aggregations often persisted after the disappearance of the sun; but probing in the pool with a thermocouple disclosed small temperature gradients, which resulted from earlier insolation.

The behaviour of pupae was essentially the same as that of larvae with a few exceptions. Pupae invariably spent more time at the surface of the water; the intermittent movement to lower depths to avoid intolerably high surface temperatures was less evident. Aggregations were usually less clearly defined in relation to horizontal temperature gradients.

Relation of Solar Radiation to the Selection of Environmental Temperature by Larvae in a Pool

The coefficients of correlation between solar radiation, the mean one-inch temperature, and the differential between the mean one-inch temperature and the preferred ambient temperature of each of the two aggregations in the two pools, for both increasing and decreasing insolation, are given in Table III.

In geophysical investigations it is generally considered that a correlation coefficient (r) is significant if it exceeds three times its probable error ($P < .05$); but some climatologists contend that an acceptable coefficient should not be less than six times its probable error ($P < .01$) unless it is confirmed by physical reasoning or other independent evidence (Tuttle and Satterley, 1925, pp. 262-263). The more rigorous of the two statistical limits was used in this investigation in view of the importance of systems of behaviour in estimating environmental temperatures and in predicting dates of emergence. The correlation between intensity of solar radiation and the mean one-inch temperature was negative and not significant. However, the interpretation of this negative correlation should be distinguished from the probability of a positive correlation between pool temperature and cumulative solar radiation in a purely physical system. In terms of a purely physical system the representation of variations in solar radiation in relation to the complete range of one-inch temperatures is biased. Since the correlation of solar radiation with mean one-inch temperature

Fig. 6. Daily variations in the micro-environmental temperature selected by aggregations of mosquito larvae in relation to the variations in incident solar radiation and the maximum, minimum, and mean temperatures one inch below the surface of the pool: A, on bright, sunny day with cumulus cloud formations; B, on clear, sunny day; C, on sultry, sunny day with haze gathering in the afternoon and sky overcast in late evening.

TABLE III

The coefficients of correlation between solar radiation and the temperatures associated with the behaviour of mosquito larvae in a natural pool. Numerals in parentheses are the ratios of the coefficients to their probable errors. Coefficients for increasing and decreasing radiation are shown in roman and italics respectively

	Solar radiation	Mean one-inch pool temperature	Differential between mean pool temperature and ambient temperature of aggregation I	Differential between mean pool temperature and ambient temperature of aggregation II
Solar radiation.....	-	-0.080 (0.7)	+0.512 (6.1)	+0.687 (11.2)
Mean one-inch pool temperature.....	-0.213 (1.9)	-	-0.365 (3.6)	-0.334 (3.3)
Differential between mean pool temperature and ambient temperature of aggregation I ..	+0.598 (8.0)	-0.451 (4.9)	-	+0.717 (12.7)
Differential between mean pool temperature and ambient temperature of aggregation II ..	+0.536 (6.5)	-0.361 (3.6)	+0.865 (29.7)	-

was restricted to the presence of aggregations of larvae or pupae, the coefficients between these two factors do not constitute random representation as individual variables in the physical system, but rather only so far as they are related to the formation of aggregations of larvae or pupae; but the lack of correlation between solar radiation and the mean one-inch temperature is biologically significant in the interpretation that pool temperature and solar radiation affect the behaviour of mosquito larvae independently.

The correlation between solar radiation and the differential between mean pool temperature and the ambient temperature of the aggregation was significant for both increasing and decreasing insulation; the coefficients 0.512, 0.687, 0.598, and 0.536 approach one another in magnitude and suggest that the same constituents of solar radiation were influencing the behaviour of the aggregation in both the shaded and the insulated sectors of the pool. This suggestion was supported further by the very high correlation between (i) the differential between the mean pool temperature and the ambient temperature of the aggregation in direct sunlight and (ii) the differential between the mean pool temperature and the ambient temperature of the aggregation in the shade. The coefficients for decreasing and increasing insulation (0.717 and 0.865 respectively) were the highest among all the correlations and indicate the importance of solar radiation in separating the two aggregations. The correlation between the mean one-inch pool temperature and the differential between the mean one-inch temperature and the ambient temperature of the aggregation was not significant; this indicated that the behaviour of the larvae depended little on the mean one-inch temperature of the pool.

TABLE IV

A comparison of the mean temperature one inch below the surface of a pool with the average differential between the mean temperature one inch below the surface and the microenvironmental temperature of the aggregation

Mean temperature one inch below surface, $\pm 1^{\circ}\text{F}.$	Aggregation in direct sunlight		Aggregation in shade	
	No. of observations	Average temperature differential* $^{\circ}\text{F}.$	No. of observations	Average temperature differential* $^{\circ}\text{F}.$
34.....	5	1.1 ± 0.9	6	0.5 ± 0.9
36.....	5	4.5 ± 2.2	5	2.5 ± 1.2
38.....	4	2.6 ± 1.8	3	2.6 ± 0.6
40.....	4	3.1 ± 2.2	4	1.5 ± 0.9
42.....	5	2.2 ± 1.2	5	2.3 ± 0.7
44.....	4	3.1 ± 2.5	5	2.7 ± 1.4
46.....	4	1.9 ± 0.4	3	1.2 ± 0.4
48.....	5	2.1 ± 1.1	5	1.8 ± 1.0
50.....	5	2.2 ± 1.7	5	0.80 ± 0.9
52.....	7	1.6 ± 1.4	9	0.83 ± 0.4
54.....	5	1.3 ± 0.4	5	1.0 ± 0.9
56.....	6	0.20 ± 1.3	7	0.80 ± 1.2
58.....	6	-0.22 ± 1.1	7	0.61 ± 0.3
60.....	6	-0.62 ± 1.3	6	0.04 ± 0.2
62.....	5	-2.3 ± 0.8	5	0.0
64.....	6	-3.0 ± 1.1	5	0.0
66.....	5	-3.3 ± 1.0	5	0.0
Total	87		Total	90

*The average of the differential between the mean one-inch temperature and the ambient temperature of the aggregation with its standard deviation.

For practical application, it was important to determine whether a graphic relation exists between the behaviour of the larvae and the environment selected and whether it influences rate of development. This type of information is condensed in Table IV. The average of several differentials between the mean one-inch temperature and the ambient temperature of larvae at the centre of the aggregation is shown for each range of 2 degrees for temperatures between 33 and 67°F. There was considerable variability in the temperature differentials since the solar radiation was variable. Smoothed curves representing the ambient temperatures selected by the two aggregations of larvae in relation to the mean one-inch temperature of the pool are shown in Fig. 7. At low mean one-inch temperatures, the ambient temperatures of mosquitoes were considerably higher than the mean one-inch temperature; at mean one-inch temperatures above 60°F., they were lower and the aggregation in the shade dispersed. Both curves in Fig. 7 indicate that the mean one-inch temperature (and hence the surface temperature) in a pool at far northern latitudes does not represent the actual environmental temperature of *A. communis*.

Discussion

Behaviour similar to that observed for *A. communis* in natural pools at Fort Churchill does not appear to have been described previously. The differences reported in this paper are probably related to conditions of insolation peculiar to mosquito pools at far northern latitudes. The interpretation of the behaviour system observed is supported by previous laboratory investigations on other species of mosquitoes. The presence of two distinct aggregations of larvae is

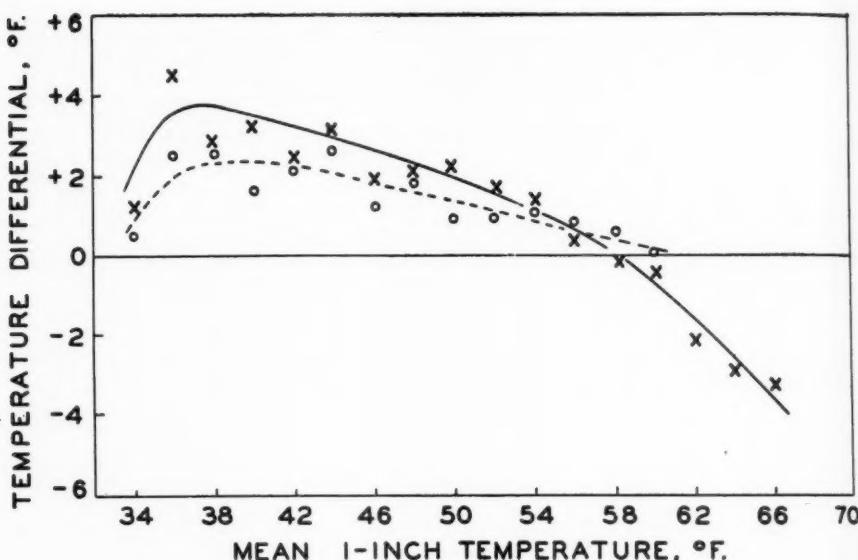


Fig. 7. The micro-environmental temperatures selected by aggregations of mosquito larvae at various mean temperatures one inch below the surface of the pool (solid line, aggregation in direct sunlight; broken line, aggregation in shade).

attributable to orientation in response to external stimuli. A combination of at least two stimuli is involved: (i) solar illumination (particularly in relation to the effect of its dynamic as opposed to its quasi-static state) and (ii) solar heating of water in relation to horizontal and vertical temperature gradients. Temperature gradients in the pool stimulated the larvae to select their preferred ambient temperature. The presence of both horizontal and vertical temperature gradients caused a three-dimensional displacement of larvae to two points of aggregation in preferred sectors of pools when the perimeters were reasonably regular. The clockwise daily progression of insolation around the pool produced a warm sector which advanced with the insolation. The warm sector extended beyond the trailing edge of the constantly advancing insolated sector into the shaded sector throughout most of the day. Straggling larvae in the insolated sector, upon coming to the edge of the shaded sector, became positive to gravity or negative to light (or simultaneously positive to gravity and negative to light) as they were subjected to a suddenly diminishing intensity of light. Some aspects of this behaviour have been described by Folger (1946) and Holmes (1911) for mosquito larvae in the laboratory and for other invertebrate animals by Taliaferro (1920), Dolley and Wierda (1929), and Mast (1924). Holmes (1911) showed in laboratory experiments that mosquito larvae were normally negative to gravity but became positive during and immediately after sudden changes of light intensity. In more elaborate experiments with *Culex fatigans* Wd., Folger (1946) showed that the behaviour of the larvae was influenced also by a phototactic response. When the orientation of the source of light was manipulated in relation to the force of gravity the larvae exhibited a definite phototaxis. However, neither Folger nor Holmes mentioned any effect of other important environmental

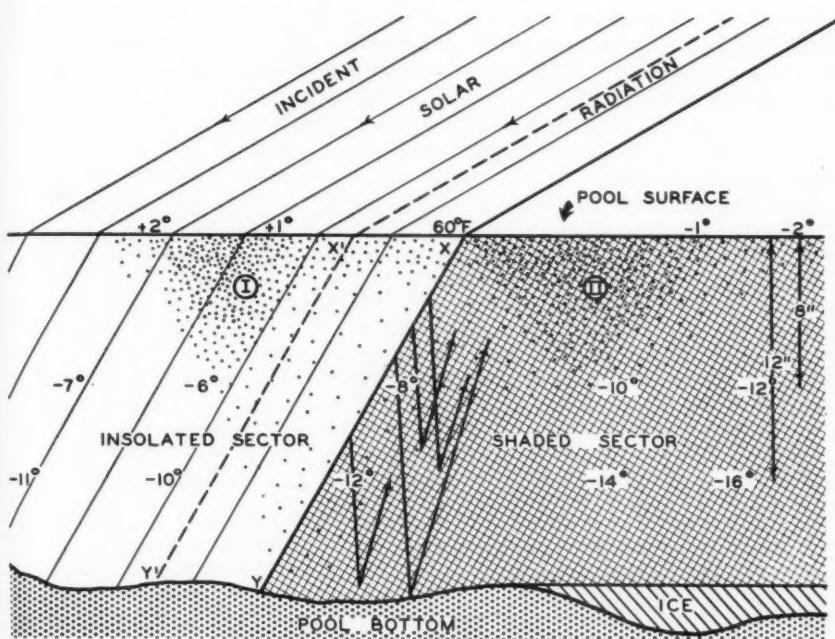


Fig. 8. Diagram of a short vertical cross-section through the boundary (xy) between the insulated and shaded sectors of a pool showing (1) the relative positions of the two aggregations of larvae, (2) the general arrangement of horizontal and vertical gradients, (3) the concentration of geotactic movement of larvae at the interface between the two sectors and (4) the transfer of straggling larvae (represented by bent arrows) from the aggregation in the insulated sector to the one in the shade. (See text).

factors, such as temperature, on the responses of mosquito larvae to gravity or light. In nature, at the trailing edge of the insulated sector, the light stimulus was probably predominant to the stimulus of the horizontal temperature gradient between the point of maximum heating and other parts of the pool, including the shaded sector. The light intensity in the shaded sector, although considerably less than in the insulated sector, was quasi-constant and the stimulus of a temperature gradient was effective for mosquitoes conditioned to the intensity of illumination in the shade.

The combined effects of light and temperature on the responses of mosquito larvae are shown in Fig. 8. The diagram shows a short vertical cross-section through the plane (xy) that represents the interface between the sunlit and shaded sectors of a pool. Aggregation I represents larvae conditioned to quasi-constant high light intensity in the insulated sector whereas aggregation II represents those conditioned to quasi-constant low light intensity in the shaded sector. Under quasi-constant light conditions the larvae are constantly attracted toward the surface and to the left by their response to favourable temperature gradients. Response to vertical and horizontal temperature gradients alone would lead to formation of a single aggregation at the point of maximum heating; but a sudden change of light intensity provides a positive geotaxis at the interface between the insulated and the shaded sectors. Larvae that contact the interface (along

xy) become positive to gravity or react negatively to light and work their way vertically downward to the bottom of the pool. Thus they automatically arrive in the shaded sector by the nature of the angle that refracted light rays constantly make with the vertical plane. As they become conditioned to the quasi-constant low intensity of light they once more respond normally to temperature gradients. Larvae trapped in the shaded sector consequently join aggregation II when they eventually move again toward preferred temperatures at the surface. Once trapped in the shaded sector larvae are forced by their positively geotactic reaction at the barrier xy to remain in aggregation II until light intensity becomes more uniform over most or all of the pool. At high latitudes the interface (xy) between the shaded and insolated sectors advances continuously in a clockwise direction around the pool from a point on the southwest side in early morning to a point on the southeast side in late evening. As a result of the change in the direction of insolation the horizontal temperature gradients vary in the pool to conform more or less with the general relation of temperatures shown in Fig. 8. Thus as the boundary xy moves forward ($x'y'$) the straggling larvae that fail to keep their position in aggregation I near the centre of maximum heating in the constantly shifting horizontal temperature gradient are gradually trapped in the shaded sector by positive geotaxis at the trailing edge of the insolated sector.

Aggregation II was formed by stragglers from aggregation I and it was maintained by temperature gradients until the mean surface temperature of the pool rose above the preferendum of the larvae (60-62°F. for *A. communis* at Churchill). This hypothesis was supported by the following observations: (a) the aggregation in the insolated sector always formed well in advance of the aggregation in the shade, (b) the aggregation in the shade dispersed when the temperature gradient between the shaded and insolated sectors disappeared in late afternoon, (c) the density of the aggregation in the insolated sector reached its maximum before noon and gradually decreased during the remainder of the day; by comparison the aggregation in the shade gradually increased in density until it suddenly dispersed in late afternoon, and (d) greatest geotactic movement was consistently observed among larvae between the two aggregations at or near the interface between the insolated and shaded sectors.

The presence of the aggregation in the insolated sector probably depended on a balance between (i) positive phototaxis in light at quasi-constant high intensity (causing the larvae to be negative to gravity and positive to light) and (ii) response to vertical and horizontal temperature gradients; this would also explain the presence of the aggregation at lower depths when the mean one-inch temperature was above the apparent preferred level of 60-62°F. Folger (1946) concluded from laboratory experiments that larvae were positively phototactic in variable, low or constant light intensities and negatively phototactic in very high or suddenly changing intensities. This conclusion is verified by the behaviour of *Aedes* larvae in natural subarctic pools; but the orientation of larvae to form aggregations in response to geotactic and phototactic stimuli is modified by temperature gradients. Nielsen (1953) described peculiar aggregations of the larvae of *Aedes taeniorhynchus* (Wd.) in Florida pools but offered no explanation for this type of behaviour.

The mean one-inch temperature, and any other empirically selected temperature near the surface of the pool, was representative of the ambient temperature of the larvae for a very small portion of their development, i.e., only while it coincided with the normal temperature preferendum (60-62°F., Fig. 7) of the species. Theoretically, mosquito larvae may select their preferred temperature

in a pool irrespective of very high surface temperatures provided that the pool maintains suitable horizontal or vertical temperature gradients and that surface temperatures are not high enough to be rapidly lethal.

The ability of mosquito larvae and pupae to absorb solar radiation directly when they are near the surface was not considered. Considerable absorption of direct or nearly direct radiation may be expected, especially by pupae, which spend more time at the surface than do larvae. It is possible that the relation between the in-going and out-going heat radiation in the animal itself affects its behaviour in the selection of its preferred temperature. This factor may be responsible for the variation found in the observations already discussed.

The pools described appear to have many characteristics common to the moorland pools described by Carpenter (1931, pp. 216-220) and Harnish (1926). Carpenter states, 'The peculiar rigours are oxygen-poverty, lime-scarcity, temperature-instability, acid reaction of the water *per se*, and peculiar chemical conditions. Any one of these factors may be operative in keeping out particular species; most probably they work in combination.' Although Carpenter described the probable significance of such rigorous physical factors as extreme temperature-instability in relation to survival of various fauna, there is apparently no record of behaviour systems that are peculiar to the animals that inhabit the moorland type of pool.

The daily variation in vertical temperature gradients in pools with subjacent permafrost is very different from that in pools in temperate or tropical areas. The general pattern of temperature variation shown in Fig. 4 indicates that at the point of maximum heating the vertical temperature gradient becomes steeper at two depths, (i) near the surface and (ii) near the permafrost at the bottom. The water reaches its maximum density at 39.2°F. and, provided that solar radiation does not heat the lower layers of water above that temperature, there is no convection between the top and the bottom of the pool. Theoretically, however, there would be convection between the 39°F. level and the top of the permafrost. The temperature gradient from the 39°F. level to the surface would be maintained by the thermal conductivity of the water and insolation at the surface except at the periphery of the pool, where radiant heating of submerged vegetation or mud would support a complex of small convection currents. The form of the curves changes for vertical temperature gradients, especially for the lower levels, as the permafrost melts. When the subjacent permafrost breaks contact with the bottom of the pool, vertical temperature gradients approach in form those common to temperate areas. Later in the summer, provided that the permafrost has receded several inches below the bottom of a pool, the steepness of the curves OA and OB (Fig. 4) disappears at the bottom levels. The level of maximum density fluctuates not only during the season but from day to day. This fluctuation depends on the balance between (i) the cooling influence of the subjacent permafrost and (ii) the warming influence of insolation of the water and of thermal conductivity of the air at the surface of the pool.

Boyd (1929) described the physical factors influencing the distribution of North American anophelines in North Carolina; but his description of the thermal conditions of pools was restricted to surface temperatures. Missiroli (1953) described the thermal characters of the breeding places of *Anopheles plumbeus* Steph.; but the thermal variations that he mentioned were related to the restriction of certain species to particular pools. An excellent micro-climatological account of temperature variations in small bodies of water is given by Geiger (1941, translation 1950, pp. 153-159) for both temperate and tropical zones. Geiger

states, ". . . as water surfaces diminish in size the water temperatures are likely to approach those of dry land while still retaining their peculiar characteristics." This statement is apparently true for the subarctic mosquito pools; the large variations in pool temperatures are presumably associated with the extreme fluctuation in temperatures at the ground surface which is subject to heating by direct solar radiation and to cooling by subjacent permafrost and by radiation of heat to space.

Pichler (1937) made a series of measurements at 650 m. above mean sea level in temperate climate in a shallow pool with an area of 12 sq. m. and a maximum depth of 40 cm. At a depth of one centimeter he found a daily temperature range of more than 10 degrees Centigrade. It decreased with depth to about 4 degrees at a depth of 40 cm. The temperature curves were of approximately the same form as those in Fig. 4 for the upper levels but, from Pichler's description, the effect of bottom cooling, which has a very large influence on subarctic pools at any time of the day, is evident in temperate pools to a lesser degree and only during the hours of low or zero insolation, i.e., about 7 p.m. to 3 a.m. An isothermal layer that forms below the surface after sunset and increases in thickness until sunrise is restricted in subarctic pools to the water levels above the 39°F. level unless the pool is subjected to near-freezing air temperatures. Apparently the physical phenomena affecting the microclimate of small pools in temperate and subarctic areas differ not in their fundamental character but rather in the degree of their influence.

Summary

Investigations on behaviour of the immature stages of *A. communis* (Deg.) under natural conditions at northern latitudes showed the following:-

1. The system of behaviour of the larvae was related to (a) conditions of insolation peculiar to northern pools and (b) horizontal as well as vertical temperature gradients.
2. The low angle of inclination of the sun to the horizontal contributed mainly to the peculiar conditions of light and temperature.
3. The balance between kinetic, or tactic, stimuli of light and temperature appeared to be responsible for the formation of one or two, but not more than two, principal aggregations of larvae in pools that were partially insolated and regular in outline.
4. Underlying permafrost usually modified the temperature fluctuations in a pool and was partially responsible for extreme vertical and horizontal gradients when any one part of the pool was intensely insolated.
5. Mean temperatures near the surface of a pool were significantly representative of the ambient temperature of larvae for a very short portion of the total period of development in the subarctic. When the mean temperature at one inch below the surface of the water was below the species preferendum, the larvae aggregated in areas as much as four degrees Fahrenheit above the mean temperature. Larvae aggregated temporarily at lower depths in the pool when surface layers of water exceeded the preferendum.
6. The system of behaviour indicated that time-temperature relations would be seriously inadequate in estimating rate of development under conditions peculiar to far northern latitudes unless corrections were made for the behaviour of the animal.

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Insects of Potential Economic Importance New to Canada, 1954: a Review¹

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A considerable number of insect species of potential economic importance new to Canada, some being new to North America, have been recorded in the Canadian Insect Pest Survey since new records were reviewed (McNay, 1955). These and others, mainly from 1954 records, are brought together in this paper. Two new mite species are included. Sources of information include Survey reports from officers of the Entomology and Plant Protection divisions, provincial entomologists, and other co-operators; *The Canadian Entomologist*; *The Canadian Insect Pest Review*; *Proceedings of the Entomological Society of British Columbia*; and the *Bi-monthly Progress Report* of the Forest Biology Division, Canada Department of Agriculture.

Insects New to North America

This section includes records of insects that had not previously been known to occur or to be established in North America.

Four new species of plant bugs of the genus *Liocoris*, previously considered to be species of the genus *Lygus*, were described by Kelton (1955). *L. rufidorsus* was described from specimens collected at several points in Alberta and Saskatchewan from 1929 to 1952. Specimens from White Fox, Sask., were taken on alfalfa. *L. unctuosus* was described from specimens collected at numerous points in Western Canada from 1915 to 1952; Moose Factory, Ont., in 1949; Rupert House, Que., in 1949; and Fort Simpson, N.W.T., in 1950. Specimens from Torch River, Sask., were taken on pineapple-weed, *Matricaria matricarioides* (Less.) Porter. *L. borealis* was described from specimens taken at many points in Alberta and Saskatchewan from 1913 to 1952; Aweme, Man., in 1922; Rampart House, Yukon, in 1951; and Yellowknife, Fort Simpson, and Reindeer Depot, N.W.T., from 1948 to 1950. Specimens from White Fox, Sask., were taken on alfalfa. *L. solidaginis* was described from specimens collected at several points in Alberta from 1930 to 1952 and Saskatchewan from 1950 to 1952. Host plants included wolfberry, *Symporicarpos occidentalis* Hook.; goldenrod, *Solidago* sp.; hounds-tongue, *Cynoglossum boreale* Fern.; Canada thistle, *Cirsium arvense* (L.) Scop.; and snowberry, *Symporicarpos albus* Blake. This species is very abundant on snowberry in the spring and on goldenrod in the fall.

Larvae of *Yponomeuta padella* L., commonly called the ermine moth, were collected on *Euonymus* sp. in mid June in a nursery at Agincourt, Ont. Later, approximately 50 cocoons were found in the area. In Europe this insect feeds only on species of *Euonymus* (McNay, 1954).

A geometrid, *Calocalpe prunivora* was described from eastern North America by Ferguson (1955). In Canada it was taken in Nova Scotia and in southern areas of Quebec and Ontario. The larvae were found always in large nests formed by tying the leaves on terminal shoots together and only on wild black cherry, *Prunus serotina* Ehrh. Although the species has two overlapping broods each season in the southern part of its range in North America, there is probably only one in most or all of its range in Canada.

Three species of *Latalus* (Homoptera: Cicadellidae) were described from Canada by Beirne (1954): *L. bultus* from Manitoba, *L. bistrionicus* from British

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Columbia, and *L. personatus* from many points from the Rocky Mountains eastward to the Province of Quebec. Three other species of leafhoppers were described from Canada by Beirne in 1955. *Dicranoneura frigida* was taken on tundra at Deer River and at Farnsworth Lake near Churchill, Man., in 1952. *Athysanella (Amphipyga) longicauda* was collected at several points in eastern Ontario and western Quebec from 1927 to 1954 and appears to be confined to Eastern Canada. *Lonatura crocea* was taken at Bateman, Sask., in 1939; Elbow, Sask.; in 1951; and Aweme, Man., in 1930.

Other leafhopper species taken on grasses and sedges in northern non-agricultural areas of Canada, and therefore of possible but doubtful economic importance, included the following: *Streptanus marginatus* (Kirsch.), *Psammotettix lapponicus* (Oss.), *Coulinus uladus* Beirne, *C. usnus* Beirne, *Hebecephalus mornus* Beirne, and *H. creinus* Beirne (Beirne, 1954).

The eastern North American subspecies of the barberry geometrid, *Coryphista meadi atlantica*, was described by Munroe (1954) from specimens collected in Kings County, N.S., in 1951 and at Ottawa, Ont., in 1952. It occurs sporadically in Eastern Canada and commonly in the United States. In 1952 an outbreak in the Ottawa region caused minor damage to ornamental barberry. The western subspecies, *Coryphista meadi meadi* (Packard), occurs commonly in southern British Columbia and the Cordilleran region of Alberta.

Amphorophora rubitoxica Knowlton (1954) was reported (Stace-Smith, 1954) as causing widespread chlorotic spotting of the foliage of Munger black raspberry, *Rubus occidentalis* L., in the coastal regions of British Columbia. Spotting appears first in June and by mid July virtually all plants are affected, although on some only a few leaves may be spotted.

A mite, *Typhlodromus pini* was described by Chant (1955) from specimens collected from beneath the bark of lodgepole pine, *Pinus contorta* Dougl., and white pine, *P. strobus* L., in Vancouver.

Another mite, *Zwickia gibsoni*, was described by Nesbitt (1954) from specimens collected from the pitchers of *Sarracenia purpurea* L. in sphagnum bogs in the Danford Lake area, Quebec; Aylesford, N.S.; and Mer Bleue near Ottawa, Ont.

Two northern species of mosquitoes were described by Vockeroth (1954). *Aedes (Ochlerotatus) implicatus*, previously known incorrectly as *A. (O.) impiger* Walk., was described from specimens collected at Rupert House, Que., and others were taken at several widely separated points in Canada. *Aedes (Ochlerotatus) rempeli* was described from specimens taken at Great Whale River, Que., and Padley, N.W.T.

A European pest of hawthorn and apple, *Swammerdamia lutaria* Haw. (Lepidoptera: Yponomeutidae), caused extensive damage to hawthorn in St. John's, Nfld. (Freeman, 1954).

A dragonfly, *Somatochlora brevicincta* Robert, was described by Robert (1954) from specimens collected on peat bogs in the area about Lake Mistassini, Que.

Insects New to Canada

This section includes records of insects not previously recorded from or known to be established in Canada but known to occur elsewhere on the continent.

The alfalfa weevil, *Hypera postica* (Gyll.), was found at Manyberries and 35 miles east of Milk River, Alta. (Hobbs, 1954). Subsequent surveys revealed

infestations in many isolated fields along the Milk River and at Orion, Sterling, and Cranford. The parasite *Bathyplectes curculionis* (Thom.) was commonly found, suggesting that the weevil had been present for more than one year. The weevil was found also in the southwestern and south-central agricultural areas of Saskatchewan and, as in Alberta, had probably been present for more than a year. *H. postica* has been particularly troublesome on alfalfa in west-central areas of the United States. Most damage is done to seedling stands, but when older stands are attacked serious losses may occur in both the quality and quantity of feed.

The sugar-beet wireworm, *Limonius californicus* (Mann.), caused 45 to 50 per cent reduction in the stand of sugar beets in a six-acre planting near Turin, Alta. (Lilly, 1954). The damaged crop was on low-lying, irrigated, alkaline soil. Examination of other plantings in the vicinity failed to reveal any specimens of the species. The only previous record of its presence was the finding of two specimens, probably of this species, at Taber, Alta., about 1936. The severity of the infestation, together with a history of very thin, patchy crops of wheat on the land for three consecutive years, indicated that the infestation had been present for a considerable period.

The chalcid *Spalangia rugosicollis* Ashm. parasitized up to 11 per cent of first-generation pupae of the onion maggot, *Hylemya antiqua* (Mg.), at St. Jean, Que. (Perron, 1954). This is the first record of this parasite attacking the onion maggot. The chalcid has been recorded in the United States but never on this host.

Adults of *Thrips* sp. near *fuscipennis* Hal. were collected from the blooms of blackberry and loganberry, *Rubus* spp., in the lower Fraser Valley at Huntingdon, B.C. Apparently the only published record of *T. fuscipennis* in North America is from New York in 1927 (Tonks, 1953).

A phytophagous mite, *Petrobia latens* (Müller), was collected on apple trees and cover crops in the Okanagan Valley, B.C. The species is known to be of economic importance on truck crops and grains in southern areas of the United States (McNay, 1955).

Three specimens of the gall fly *Phytophaga tumidosae* (Felt) were reared from the scarred gall of willow collected near London, Ont. (Judd, 1955).

A wood borer, *Micracis suturalis* Lec., was collected on white elm at Oldcastle, Ont. (Finnegan, 1954). The insect is known to occur in the neighbouring State of Michigan, U.S.A.

Alegina pinifoliae (Cush.) was recorded as a parasite of the lodgepole needle miner, *Recurvaria milleri* auett., in Banff, Yoho, Kootenay, and Jasper national parks (Stark, 1954). It is parasitic on the pine needle miner, *Exoteleia pinifoliella* (C' lamb.), in Massachusetts, U.S.A.

A specimen of the wheel bug, *Arilus cristatus* L., was taken in Windsor, Ont. (Boyce, 1954). The only previous Canadian record of this insect, made by Mr. W. R. Lapp, Plant Inspection Office, Windsor, was from Walkerville, Ont., a suburb of Windsor. The records indicate probable establishment in the area. The wheel bug is a beneficial insect preying on the larvae of the white-marked tussock moth, the fall webworm, the locust leaf miner, and other pests.

The black fly *Simulium rugglesi* N. & M. was reported from both Eastern and Western Canada; specimens collected in the Prairie Provinces from 1947 to 1953 indicated this species to be moderately numerous (Anonymous, 1954).

In Eastern Canada the black flies *Simulium venustum* Say and *S. bracteatum*

Coq. had both been named by earlier workers as the vectors of *Leucocytozoon simondi* M. & L., a protozoan parasite infesting the blood of waterfowl. The organism causes a disease somewhat like malaria, usually fatal to young birds. Studies by Shewell (1955) of black fly specimens in the Canadian National Collection indicated, however, that the earlier determinations were in error and that *S. rugglesi* N. & M. was responsible. This opinion was confirmed by evidence obtained in 1954. Specimens were taken in association with sickly ducklings at Maugerville and Fredericton, N.B., and Manotick, Ont., and at Fredericton 52 engorged specimens were collected from the bodies of the ducklings. Heavy losses were reported also at the Provincial Veterinary Laboratory in Manitoba, but apparently no attempt was made to obtain black fly specimens. In addition to these records there are specimens in the Canadian National Collection from several localities in Quebec, and Goose Bay, Labrador.

A female pupa of the rare and remarkable family called "mountain midges", of which there are only two recognized North American species, was taken at Jasper, Alta., in 1932 (Shewell, 1954). The pupa agreed with the description of *Deuterophlebia coloradensis* Pennak. The species is known to occur at higher altitudes of the Rocky Mountains in Colorado, Utah, and Wyoming. This, the first record of the family in Canada, extends its range northward over 500 miles on this continent and is the most northerly record for any species.

Adults of the secondary screw-worm, *Callitroga macellaria* (F.), were collected at Point Pelee, Ont., in 1954. Walley (1954) states that the insect was found in sufficient numbers to suggest that it is well established in the area. The only previous record for Canada was of a single specimen taken at Jordan, Ont., in 1919. The larvae develop on exposed carcasses and occasionally infest wounds of warm-blooded animals. The species is common in the American tropics.

The tick *Ornithodoros kelleyi* C. & K. was taken in the library of a building in Saskatoon, Sask. (Gregson, 1954). Evidence of bats in the attic of the building indicated that they may have been the hosts.

The crow flea, *Ceratophyllus rossittensis swansonii* Liu, was found in the nests of crows, *Corvus brachyrhynchos* Brehm, near Ottawa, Ont. (Holland, 1954). The species was previously taken from the long-eared owl, "*Asio wilsonianus*" (*A. otus* ssp.), at Fertile, Minn., and in Beaverhead County, Montana, U.S.A. It is believed to be widely distributed on the continent, but is probably scarce in Canada.

The staphylinid *Quedius mesomelinus* (Marsh.) occurred in large numbers in an earthworm-propagating establishment in Vancouver, B.C. (McLeod, 1954). Both larvae and adults killed and fed on immature and mature stages of *Eisenia foetida* (Savigny) but not on the eggs in the cocoons. Only freshly killed hosts were consumed.

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